SELECTED ASPECTS OF THE ECOLOGY OF NEMATODES IN BUTTERPOT PROVINCIAL PARK, AVALON PENINSULA, NEWFOUNDLAND

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A thesis
submitted to the School of Graduate Studies
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Department of Biology
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ABSTRACT

A total of 46 nematode taxa, from seven orders and 21 families, were collected from three habitats (a black spruce-moss forest, a Dryopteris-white birch forest, and a dry Kalmia heath-barren) in Butterpot Provincial Park, Avalon Peninsula, Newfoundland. These nematodes represent four feeding groups: microbial feeders, plant feeders, omnivores and predators. The vertical distribution, abundance, and seasonal dynamics of the four feeding groups, as well as selected species, are discussed.

Principal Components and Multiple Regression analyses revealed two environmental factors which correlate positively with increasing nematode numbers. Soil productivity (inferred from PC1) may have been the main factor governing nematode abundance in this study. The second Principal Component is a function of soil particle size and soil temperature.

The habitat rankings in terms of total nematode abundance were: Dryopteris-white birch forest > black spruce-moss forest > Kalmia heath barren Dryopteris]. The most abundant nematode populations, in all feeding groups, were in the topmost soil layer of all sites, although plant feeding nematodes comprised a larger percentage of the total nematode fauna in the lower soil layers. Within the topmost soil layer, nematode numbers from all feeding groups peaked in late spring/early summer and again in autumn.

Five distinct nematode assemblages within the three habitats were identified, by Cluster Analysis. Composition of the nematode fauna from the

Kalmia heath-barren was clearly distinct from that found in the two forest habitats. These latter habitats were similar in overall nematode species composition, but different soil layers within these habitats appeared to have different nematode assemblages. Discriminant Functions Analysis gave clear evidence that the five nematode species assemblages had an ecological basis.

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Table of Contents

List of Figures

List of Tables

Chapter 1

INTRODUCTION

1.1. Historical Review

Nematodes are among the most abundant multicellular animals. They may be free-living in marine, freshwater, or soil environments or be parasites of plants and animals. Ecological studies of soil dwelling nematodes have largely concentrated on plant parasitic taxa of economic importance [eg. Globodera spp. (cyst nematodes) (Godfrey, 1924; Chitwood and Feldmesser, 1948; Mai and Harrison, 1959); Ditylenchus spp. (bulb and stem nematodes) (Seinhorst, 1956); Pratylenchus spp. (root lesion nematodes) (Endo, 1959; Coen, 1967; Kable and Mai, 1968; Meagher, 1970)]. Nematode assemblages in undisturbed habitats have been almost neglected.

The majority of ecological studies, concerning both plant parasitic and free-living nematodes in undisturbed soil ecosystems, have been conducted in various habitats in temperate regions of both the northern and southern hemispheres. Forest habitats have been studied in England (Twinn, 1962; Yuen, 1966), New Zealand (Egunjobi, 1971), Germany (Bassus, 1962), Poland (Popovici 1980), and Holland (Yeates, 1972). Grasslands have been studied in England (Yuen, 1966), Bulgaria (Wasilewska, 1974), New Zealand (Yeates, 1974), and the U.S.A. (Orr

and Dickerson, 1966; Schmitt and Norton, 1972; Freckman et al., 1979), while pastures have been examined in New Zealand (Egunjobi, 1971; Yeates, 1982). Tundra habitats in the Arctic (Kuzmin, 1976), Antarctic (Spaull, 1973a, 1973b, 1973c, 1973d; Yeates, 1979), and Sub-antarctic (Bunt, 1954) have also been looked at, but boreal habitats appear not to have been dealt with.

A similar situation exists in Canada, where most nematological work has focussed on plant parasitic nematodes associated with crops of economic importance. Much work in Ontario has been devoted to such species as Pratylenchus penetrans, an important parasite of tobacco (Olthof et al., 1972; Elliot and Marks, 1972) and corn (Townshend, 1972), and Globodera avenae, a parasite of oats and corn (Johnson and Fushtey, 1966). Other work has dealt extensively with nematode associations within tree nurseries in Quebec (Sutherland, 1965, 1967) and British Columbia (Salisbury and Bosher, 1959). Studies on the ecology of plant parasitic and free-living nematodes in undisturbed ecosystems, is restricted to a few studies of grassland soils in Saskatchewan and Manitoba (Kimpinski and Welch, 1971; Willard, 1973) and apple orchards in Quebec (Ogiga, 1969, 1971; Ogiga and Estey, 1973). To date, no ecological work on soil dwelling nematodes has been carried out in Newfoundland.

1.2. Factors Affecting Nematode Distribution and Abundance

Soil dwelling nematodes, both plant parasitic and free-living, can be divided into five feeding or trophic groups (Banage, 1963; Yeates, 1967; Wasilewska, 1971; Spaull, 1973d) as follows:

1. Plant feeders - known or suspected plant parasites, plant browsers or plant pathogens.

2. Fungal feeders - nematodes known or thought to feed predominantly on filamentous fungi.

3. Microbial feeders - nematodes feeding primarily on bacteria but may eat algae, yeasts, filamentous fungi, and detritus.

4. Omnivores - nematodes with a heterogeneous diet which may include bacteria, algae, higher plants, Protozoa, rotifers, and possibly detritus.

5. Predators - feed on other members of the soil fauna such as other nematodes, enchytraeids, rotifers, tardigrades, and Protozoa.

Wasilewska (1971) has drawn attention to the fact that the line of demarcation between fungal and plant feeders is not sharply defined.

It is generally accepted that overall nematode numbers decrease with soil depth (Banage, 1966; Yuen, 1966; Yeates, 1967; Wasilewska, 1974; Ingham et al., 1985), however, variation among taxa is seen on the basis of their trophic preferences (Yeates, 1967; Wasilewska, 1974). Patterns of seasonal variation in nematode abundance are confusing and difficult to evaluate. Some researchers have denied that any consistent seasonal pattern occurs (Franz, 1942; Nielsen, 1949), while early summer and autumn peaks in nematode abundance have been noted in a variety of temperate forest habitats (Yeates, 1972; Popovici, 1980), and steady increases from winter to summer have been noted in temperate grasslands (Wasilewska, 1974) and Sub-antarctic tundra (Bunt, 1954). Among-habitat differences have been recorded by Banage (1966) who observed no seasonal pattern in nematode abundance on mineral soils but noted spring and autumn peaks on peat soils in England.

Nematode abundance and the vertical and seasonal distribution patterns of

trophic groups and individual taxa have been correlated with a number of environmental factors. Both abiotic (eg. soil moisture, soil temperature, pH, soil texture) and biotic (eg. food availability, root distribution) factors have been recognized. Of these soil moisture and temperature have received the most attention.

Adequate moisture content appears to play an important role governing nematode abundance. Various workers have reported that extreme moisture conditions affect most nematodes adversely (Norton, 1979; Dropkin, 1980). Dry conditions in undisturbed ecosystems are known to reduce overall nematode abundance (Banage, 1966; Yuen, 1966; Egunjobi, 1968; Jones, 1975), indeed desert habitats have lower numbers of nematodes than other habitats (Sohlenius, 1980).

Dry conditions affect egg hatching and nematode development (Norton, 1963). However many nematodes develop resistant eggs which can survive drought; egg hatching occurs when moisture increases (Dropkin et al., 1958). Nielsen (1949) has suggested that in moist soils nematodes are constantly active whereas in dry soils they must become periodically inactive. Cohn (1969) has suggested that increased populations of some nematodes after rainfall may be due to activation of quiescent nematodes by addition of water. Excessive moisture may reduce nematode populations through suffocation and buildup of toxic substances (Norton et al., 1971).

Many researchers have recognized the influence of soil temperature, during different seasons of the year, on populations of soil nematodes. Warmer spring

temperatures cause increased egg hatching (Elliot et al., 1980) and warmer summer temperatures have been reported to cause increases in nematode numbers (Bunt, 1954), although extremely high summer temperatures have also been shown to cause the decline of some nematode populations (Mountain and Boyce, 1958; Freckman and Mankau, 1977). Cold winter temperatures coincide with the decline of nematode populations in the Antarctic (Spaull, 1973a).

The information concerning the influence of soil pH on nematodes in undisturbed ecosystems is conflicting. Some workers have denied any correlation between nematode distribution and pH (Winslow, 1960; Egunjobi, 1968; Yeates 1968, 1973). However, Banage (1966) has suggested that acidic soils may lower nematode abundance while negative correlations between pH and particular nematode taxa have been noted by Schmitt (1969) and Norton et al. (1971). Other researchers have found positive correlations between individual taxa and soil pH (Brzeski and Dowe, 1969; Norton et al., 1971).

Soil type and texture have been reported to influence nematode distributions through their influence on nematode movement. Pore space affects nematode mobility and coarse soils have been reported to have more nematodes than do fine soils (Brodie, 1976; Elliot et al., 1980). Wallace (1958) and Jones and Thomasson (1976) point out, however, that too large pores may also restrict nematode movement.

The above abiotic factors may not directly influence nematode populations. In many, if not most cases, food availability is likely to be the predominant

influence on nematode abundance. Wasilewska (1974) has suggested that the distribution of all feeding groups depends on food availability and Bunt (1954) has suggested that higher nematode numbers during summer months are due to increased food production. Many researchers have noted that the distribution of plant parasitic nematodes depends on root distribution (Baines et al., 1959; Banage, 1966; Ferris and McKenry, 1976). Twinn (1962), Bassus (1962) and Egunjobi (1971), have reported high numbers of microbial feeding nematodes in forest soils. Changes in food availability for all trophic groups are likely to be reflected in several other aspects of the soil environment (eg. organic content) which may in turn exert a direct influence on the abiotic factors mentioned above.

To date, most studies of nematode community ecology have consisted of species lists from different habitats, with little or no attempt to define assemblages or relate occurrence of different groups of species to variation in the environment. A few studies have used clustering techniques (Schmitt and Norton, 1972) or a combination of clustering and ordination techniques (Johnson et al., 1972, 1973, 1974) to identify nematode assemblages in natural ecosystems. The occurrence of such assemblages have then been related to environmental factors.

1.3. Research Objectives

Nematode ecology in undisturbed ecosystems has not been addressed in Newfoundland and indeed knowledge of the island's nematode fauna is limited. The present study examines the nematode faunas of three representative boreal habitats in Butterpot Provincial Park, southeast Newfoundland. The specific objectives of the present research were:

1. To augment knowledge of the soil nematode fauna of Newfoundland.

2. To evaluate seasonal and vertical distributional patterns of the nematode fauna of three boreal habitats in southeast Newfoundland.

3. To evaluate the influence of various environmental factors on nematode distribution and abundance within these habitats.

4. To identify nematode assemblages within and among the three habitats.

5. To evaluate the extent to which the occurrence of such assemblages could be attributed to varying environmental factors.

Chapter 2

MATERIALS AND METHODS

2.1. Site Selection

Soil samples were collected from three habitats: a black spruce-moss forest, a Dryopteris-white birch forest, and a dry Kalmia heath-barren, all of which were located in Butterpot Provincial Park (53°W, 47°30'N) on the Avalon Peninsula of Newfoundland (Figures 2-1 and 2-2).

The black spruce-moss and the Dryopteris-white birch forests had previously been occupied by balsam fir-white birch forests, while the dry Kalmia heath-barren was probably a black spruce forest; all three sites are believed to have originated after fire (Roberts, 1977). Average tree height in the black spruce-moss forest was 11 metres, and the average age was 60 years. Trees of the Dryopteris-white birch forest were 4.5-7.5 metres high and approximately 70 years old. Complete site descriptions, including vegetation lists, are presented in Appendices A, B, and C.

Figure 2-1: *Map of the Avalon Peninsula,* Newfoundland indicating the location of Butterpot Provincial Park.

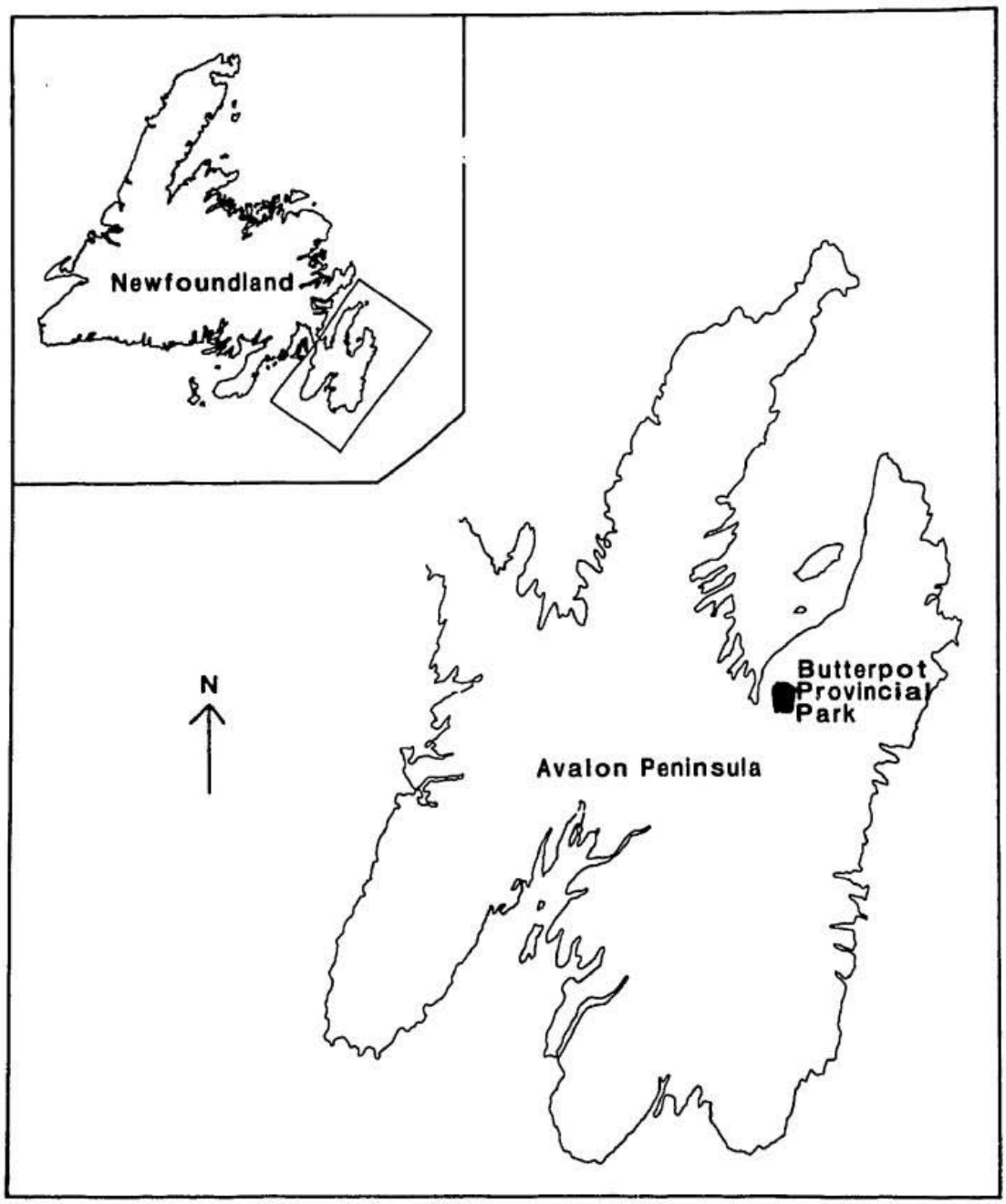
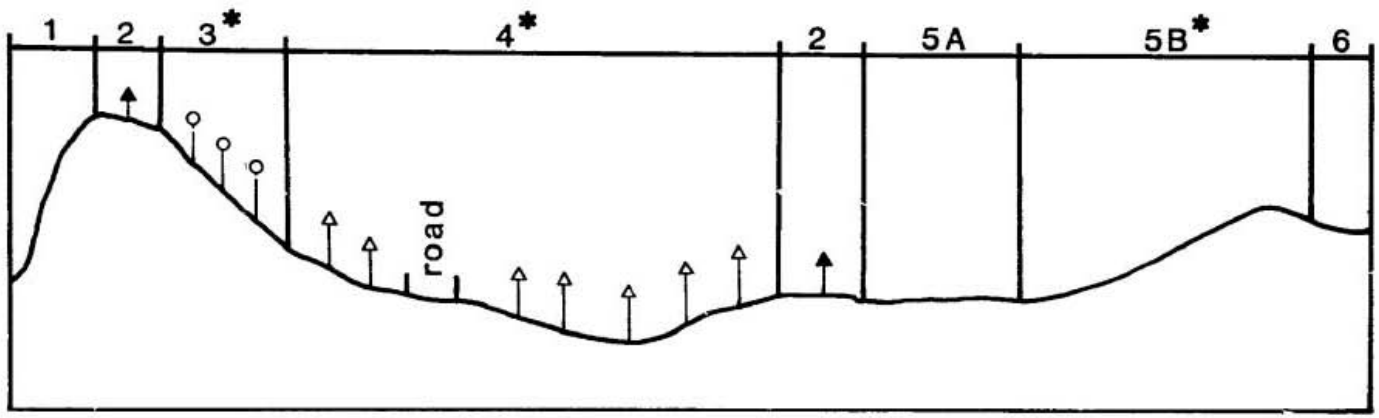

Newfoundland
N
Butterpot
Provincial
Park
Avalon Peninsula

Figure 2-2: Diagrammatic profile through Butterpot Provincial Park showing positions of study sites (from Roberts, 1983).



1 Rock Barren

2 Softwood Scrub Forest

3* Dryopteris–White Birch Forest

4* Black Spruce Moss Forest

5A Kalmia Heath Barren (wet)

5B* Kalmia Heath Barren (dry)

6 Sphagnum–Sedge Blanket Bog

* SAMPLE SITES USED IN STUDY

2.2. Soil Sampling

At 6 week intervals, from mid-May until the beginning of November (in 1986 and 1987), five soil cores were taken from within the same 10 m^2 area, at each site. Cores were approximately 10 cm. in diameter and 30 cm. deep and were removed using an auger. Cores from the black spruce-moss forest and dry Kalmia heath-barren were subsequently divided subcores based on the following soil horizons (proceeding downwards from the surface (Figures 2-3 and 2-4)).

- FH: contained both partly decomposed organic material (felt) and organic material whose original structures were unrecognizable (humus) (Wells and Heringa, 1972).

- Ae: a mineral horizon near the surface characterized by the removal of either clay, iron, aluminum or organic material individually or in combination (Wells and Heringa, 1972).

- B: a mineral region of maximum accumulation of materials such as silicate clays and iron and aluminum oxides. These may have moved down from the upper layers or may have formed in place (Brady, 1974).

In addition to the above horizons, soil cores from the Dryopteris-white birch forest also included the uppermost L (litter) layer (original structures of the organic material were easily recognizable (Figure 2-5)). These subcores were placed in plastic bags, labelled, and stored at 5-10°C (Barker, 1985) until extraction could be completed (within a week of collection).

Figure 2-3: Soil profile of black spruce-moss forest.

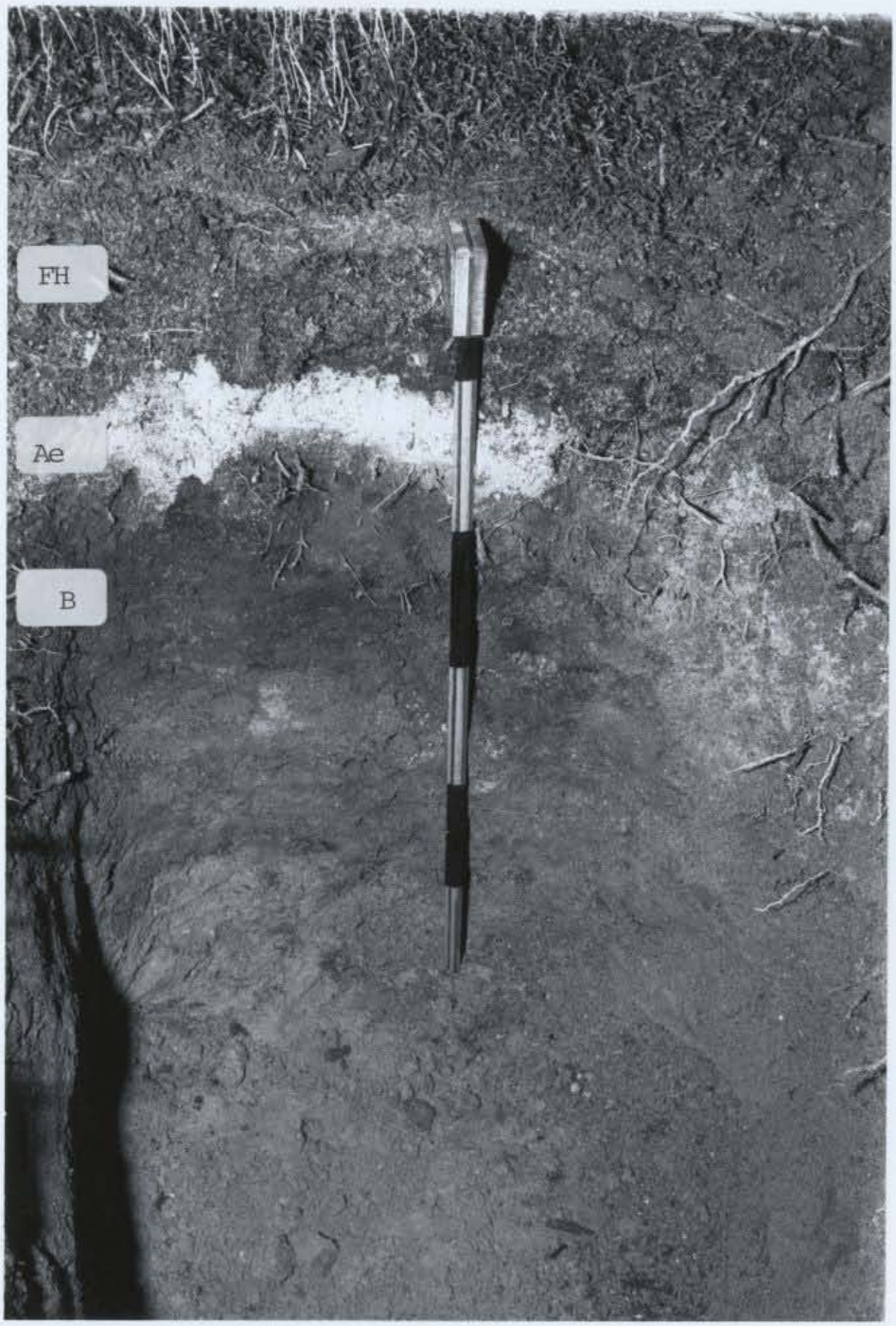

FH
Ae
B

Figure 2-4: Soil profile of dry Kalmia heath-barren.

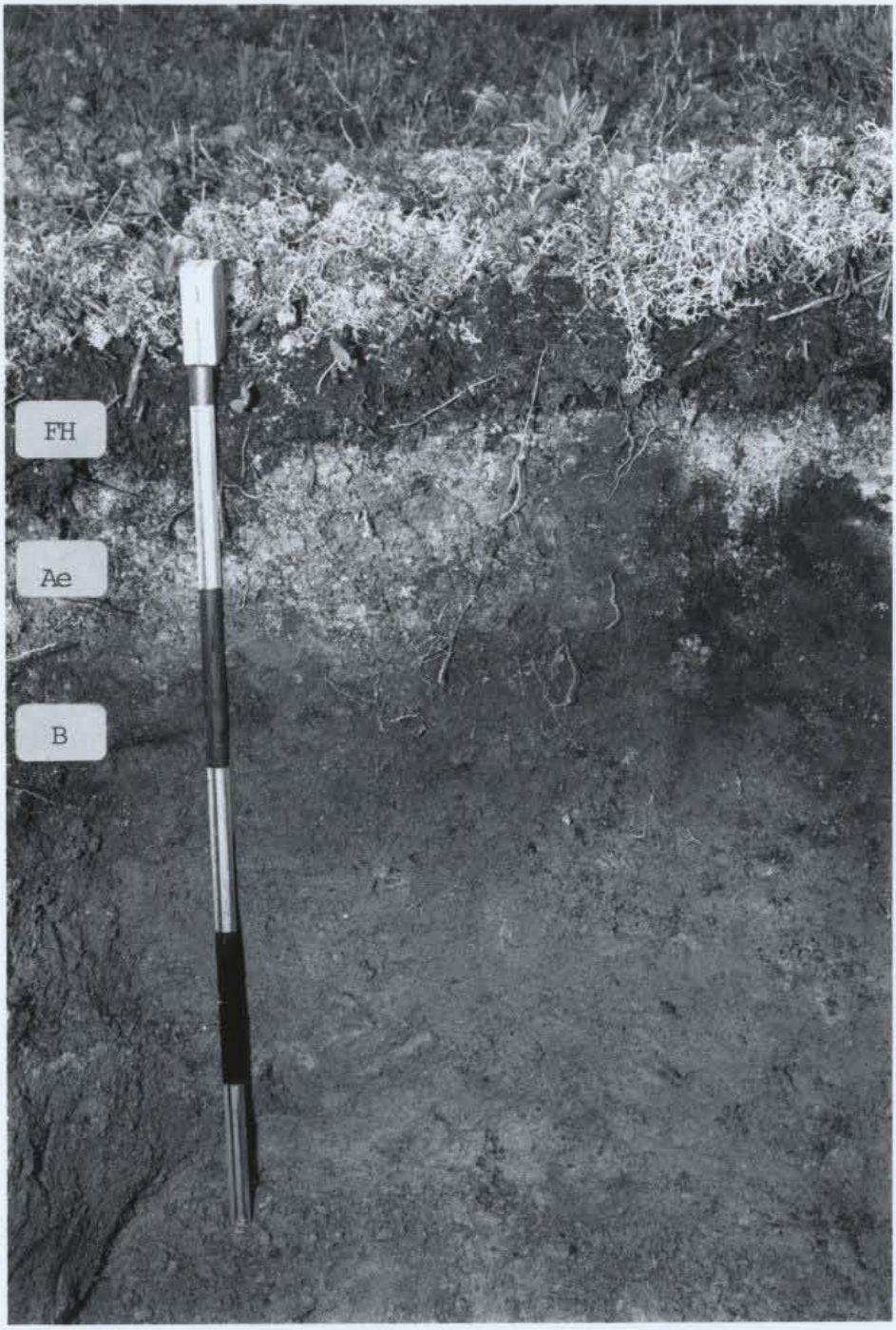
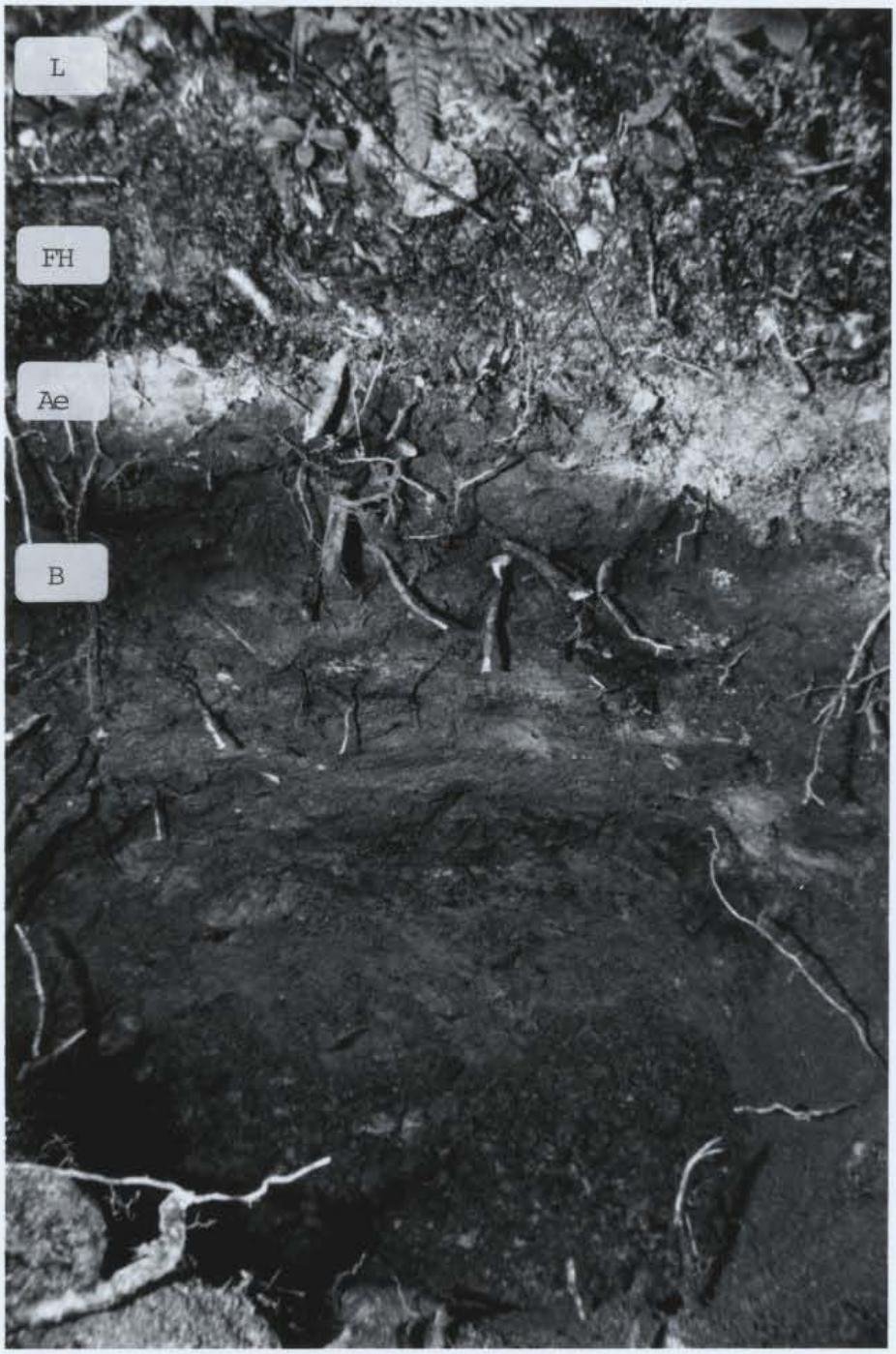

FH
Ae
B

Figure 2-5: Soil profile of Dryopteris-white birch forest.


L
FH
Ae
B

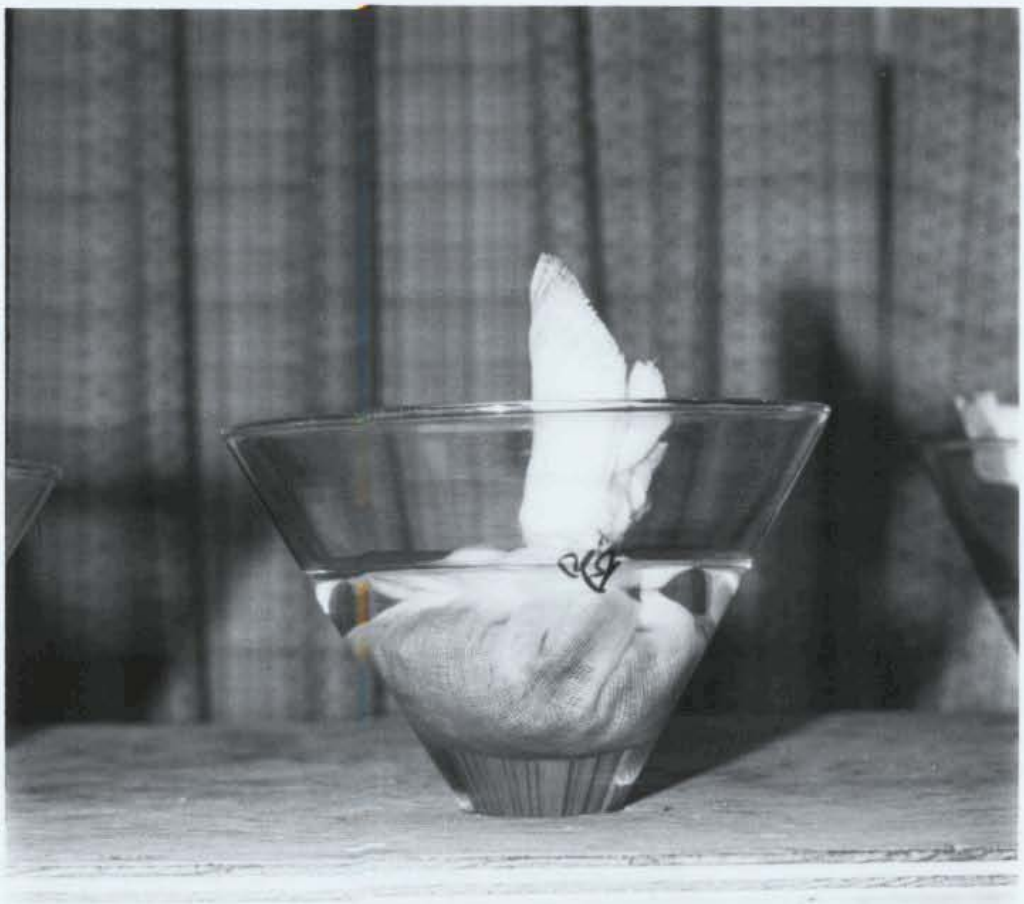
2.3. Nematode Extraction

A Baermann funnel technique was used to recover nematodes from soil subcores (Flegg and Hooper, 1970). A baermann funnel, supported in a wooden block, was filled with water. One hundred c.c. of soil were placed in a square of cheesecloth (hole size 1 mm) which was tied at the top (Figure 2-6). The soil was gently submerged in the water and left for 18-24 hours at 15°C (Goodey, 1963). During this time nematodes emerged from the soil and sunk to the bottom of the funnel. The water was then removed from the funnel stem and the total number of nematodes present was counted. For subcores that were heavily populated, nematode numbers were estimated using 1 ml or 0.1 ml dilutions. The extraction efficiency of this method was similar for all soil samples but only nematodes that were motlile were recovered.

2.4. Fixing and Processing of Nematodes

Nematodes were transferred to a drop of water on a depression slide using a handling needle. The handling needle was constructed by attaching a moderately thin (No. 1 or 2) insect pin to a wooden handle, 12 cm. in length and 2 mm. in diameter. The insect pin was bent slightly at the tip. In heavily populated subcores, nematodes were transferred by sucking up small amounts of them with a 2 ml pipette. Specimens were killed by heating the slide over a lighted match for four to six seconds (Hooper, 1970). Nematodes were immediately fixed in F.A. 4:1 (10 mls formalin (40% formaldehyde), 1 ml glacial acetic acid, 89 mls distilled water) for at least 24 hours (Goodey, 1963). Nematodes were dehydrated using Seinhorst's glycerol-ethanol method (Goodey, 1963) (Appendix D) and were left in pure glycerine.

Figure 2-6: Photograph of Baermann funnel used to extract nematodes.



2.5. Permanent Mounts

Nematodes were sunk in a drop of glycerine on a clean slide. Three small pieces of glass wool (0.3 mm in diameter) were used to support the edges of the 18 mm round coverslips to prevent crushing of the specimens. The coverslip was sealed by ringing it with two coats of clear nail enamel. Nematodes were identified to genus and where possible to species using the keys of Goodey (1963), Thorne (1974), and Siddiqi (1986). Identifications were verified by Dr. B.A. Ebsary and Dr. R.V. Anderson at the Biosystematics Research Unit in Ottawa, and by Dr. M. R. Siddiqi at the Commonwealth Institute of Parasitology, St. Albans, England. They were then assigned to one of the following feeding groups: predators, plant feeders, microbial feeders or omnivores (Banage, 1963). Assignment to a particular feeding group was based on morphological structures and information found in the literature.

2.6. Estimation of Nematode Abundance

For each subcore collected in 1986 and 1987, approximately 100 nematodes (adults and juveniles) were mounted and identified. For subcores containing less than 100 nematodes all specimens were mounted.

When mounting nematodes collected in 1986, an attempt was made to recover as many different nematode taxa as possible. Since this made it impossible to compare frequency among taxa, 1986 data were recorded only as present/absent. Data for each of the 5 subcores was pooled across the five subcores of each horizon at each site and time. Thus the presence/absence of nematodes in 500 c.c. of soil was recorded.

Nematodes collected in 1987 were identified and counted in order to estimate the relative abundance and importance of different taxa within each horizon at each site and time. Nematodes were thus mounted at random (Yeates, 1967). Nematode numbers within each taxon, obtained from the mounted specimens, were pooled. The total number of nematodes in each taxon was then estimated using percentages obtained from the pooled data and the total nematode numbers counted in 500 c.c. of soil.

2.7. Soil Analyses

In 1986 an extra soil core was collected from each site at each sampling time and was divided into subcores as described in Section 2.2. These subcores were used for chemical analyses of the soil. At the time of collection, temperature of each horizon at each site was recorded using a temperature probe.

The pH of each subcore was measured using the Sticky-Paste Method (McKeague, 1978). A saturated soil paste was prepared (ratio of soil:distilled water at approximately 1:1) and let stand for one hour. The pH was measured using a single electrode digital pH meter (Fisher Accumet , model 805 MP).

One hundred to 200 g of soil per subcore were placed in a pre-fabricated cardboard box (20 cm in length, 15 cm wide, and 10 cm deep), and allowed to dry in a drying oven. The moisture content was calculated as the difference between dry and wet weight divided by dry weight. In order to estimate particle size >2mm, the soil, once completely dried, was ground (in a mortar and pestle) as finely as possible and sieved twice through a 2 mm sieve. Particles passing through the sieve were used for further analyses.

The percentage of organic matter in each subcore was measured by drying one gram of soil in an oven at 100°C for 16 hours to remove any moisture. Subsequently the soil was placed in a muffle oven at 475°C for approximately 16 hours. This process is referred to as ashing. The weight difference between drying and ashing represented the organic content which was burned off.

Available N was extracted by steam distillation using a KCl solution while available Na, Ca, K and Mg were extracted using ammonium acetate (Black, 1965). The availability of P was assessed using a Molybdenum blue colorimetric method (Black, 1965). Levels of the above nutrients were measured using an atomic absorption spectrophotometer (Perkin-Elmer model 403).

2.8. Statistical Analyses

Mean numbers of nematodes/100 c.c. of soil (obtained from the 5 subcores collected from each site, horizon and time) were associated with a set of environmental variables for each horizon at each site and sampling time (Section 2.7). This data was used to evaluate nematode-environment relationships.

2.8.1. Relationship between nematode frequencies and environmental variables

Multiple Regression Analysis was used to determine the amount of variation in the mean numbers of nematodes/100 c.c. of soil that could be explained by the measured soil variables. However, examination of the among-variables correlation matrix (Appendix E) revealed a high degree of co-linearity. Data reduction by Principal Components Analysis (PCA) was therefore required in order to extract independent habitat factors (Sokal and Rohlf, 1981).

Since PCA assumes normally distributed data, and linear relationships between variables, transformations of the original measured variables were required. Data recorded as percentages were arcsine transformed (Sokal and Rohlf, 1981) and all other variables with the exception of pH (which is measured in logarithmic units) were log transformed.

All measured habitat variables were included in the PCA. A rotated (varimax) solution was used to interpret the principal components. The principal component scores for each sample were used as independent variables in a stepwise multiple regression. Both PCA and Multiple Regression Analysis were performed in SPSSX.

2.8.2. Nematode species assemblages and relationships with environmental factors

Species assemblages, and their relationships with environmental factors were evaluated following the protocol of Green and Vascotto (1978). This analysis was run on the pooled 1986 species presence/absence data and the corresponding environmental data.

A matrix of simple matching coefficients, derived from species presence/absence data, was used to cluster samples by species using the Unweighted Pair Group Method of NTSys version 1.3 (Rohlf, 1987). Very common or very rare taxa are likely to be relatively uninformative for sample clustering. Thus taxa that were found in either >85% of samples or <5% of samples were excluded from the analysis. The optimal number of clusters was

determined by plotting the dissimilarity (1/similarity) coefficient of clusters being joined against the number of clusters, as recommended by Sheard and Geale (1983). Inflection points on this line indicate optimum clustering levels since greater increases in slope occur when dissimilar groups are joined than when similar groups are joined.

Discriminant Functions Analysis (DFA) was used to examine separation, in microhabitat space, of the species assemblages defined above. Discriminant Functions Analysis assumes linear relationships among the measured environmental variables. However, for most ecological data relationships are likely to be multiplicative rather than additive and transformations are usually appropriate (Green, 1971; Green and Vascotto, 1978). Data were transformed as for the Principal Components Analysis, and a direct DFA was run using procedure DISCRIMINANT in SPSSX (Anon., 1986). A rotated (varimax) solution was used to interpret the discriminant functions. Since temperature data was not available for the litter horizon of the Dryopteris-white birch forest this variable was excluded from the analysis.

Chapter 3

RESULTS

A total of 46 nematode taxa from seven orders and 21 families, were recovered from the soil samples collected in 1986. Twenty taxa were identified to species and an additional 21 species were identified only to the level of genus. Three taxa could only be identified to family level. An additional two taxa could not be identified. These nematodes were distributed among four feeding groups as follows: predators (3), plant feeders (14), omnivores (10), and microbial feeders (17). Of the 46 taxa collected in 1986, 39 were also collected in 1987. All taxa (1986 and 1987), and the feeding group in which each belongs, are presented in Table 3-1. The authorities of all taxa can be found in Appendix F.

The total population of nematodes (in 500 c.c. of soil) occurring in each horizon, at the five 1987 sampling times are presented for each site in Figures 3-1, 3-2 and 3-3. The total population of nematodes (in 500 c.c. of soil) in each of the four feeding groups, at each sampling time in each layer are given for the three sites in Figures 3-4, 3-5 and 3-6. The relative importance (i.e. percentage of total nematode population) of each of the four feeding groups, at each sampling time in each layer is given for the three sites in Figures 3-7, 3-8 and 3-9. From these the following patterns are evident:

Table 3-1: Distribution of the 46 nematode taxa collected in 1986 and in 1987. (Site 1-black spruce-moss forest, Site 2-Dryopteris-white birch forest, Site 3-dry Kalmia heath-barren, + indicates taxon present, - indicates taxon absent)

	Site					
	1		2		3	
Year	86	87	86	87	86	87
Taxa						
Predators						
Mylonchulus brevicaudatus	+	+	+	+	+	+
Prionchulus punctatus	+	+	+	+	+	+
Mononchus sp.	-	-	+	-	-	-
Plant feeders						
Aphelenchoides sp.	+	+	+	+	+	+
Coslenchus costatus	+	-	-	-	+	-
Deladenus sp.	+	+	+	+	-	+
Ditylenchus sp.	+	+	+	+	-	+
Ecphyadophoridae	-	-	+	+	+	+
Hemicycliophora tenuis	+	+	+	+	+	+
Hirschmanniella sp.	-	-	+	+	-	-
Malenchus exiguus	+	+	+	+	+	-
Neocrossonema menzeli	+	+	-	-	-	+
Nothocriconemella sphagni	+	-	+	+	+	+
Ogma sp.	-	-	+	+	-	+
Pratylenchus penetrans	+	+	+	+	-	-
Seriespinula seymouri	-	+	-	-	+	+
Tylenchus sp.	+	+	+	+	+	+
Omnivores						
Aporcelaimellus capitatus	+	+	+	+	-	-
Diptherophora sp.	+	+	+	+	+	+
Eudorylaimus carteri	+	+	+	+	+	+
Eudorylaimus sp.	-	-	-	-	+	-
Mesodorylaimus sp.	-	-	+	-	-	-
Paravulvulus planposae	+	+	+	+	+	+
Prodorylaimus sp.	-	+	+	+	+	+

Table 3-1 continued

	Site 1		Site 2		Site 3	
Year	86	87	86	87	86	87
Thonus elegans	+	+	+	+	+	+
Tylencholaimus nanus	+	+	+	+	-	+
Tylencholaimus sp.	-	-	+	-	+	-
Microbial feeders						
Achromadora ruricola	+	+	+	+	+	+
Acrobeloides nanus	+	+	+	+	+	+
Alaimus primitivus	+	+	+	+	+	+
Bunonema richtersi	-	+	+	+	-	+
Cephalobus sp.	+	-	-	-	-	-
Eucephalobus sp.	+	+	+	-	+	-
Eumonhystera sp.	+	+	+	+	-	+
Euteratocephalus sp.	-	-	+	-	-	-
Micoletzky sp.	+	+	+	+	-	+
Monhysteridae	+	+	+	+	+	+
Plectus acuminatus	+	+	+	+	+	+
Plectus sp.	+	+	+	+	+	+
Prismatolaimus dolichurus	+	+	+	+	+	+
Rhabditidae	+	+	+	+	-	-
Teratocephalus sp1.*	+	+	+	+	+	+
Teratocephalus sp2.*	+	+	+	+	+	+
Wilsonema sp.	+	+	+	+	+	+
Unknowns						
Unidentified A	-	-	+	+	+	+
Unidentified B	-	-	+	+	-	-
Total	33	33	41	36	29	32
Total over both years	36		41		37	

* Two species of Teratocephalus were collected but could not be identified. They have been designated sp.1 and sp.2.

Figure 3-1: Seasonal changes in the population of nematodes (nematodes/500 c.c. of soil) in the three horizons of the black spruce-moss forest (Site 1) (1987).

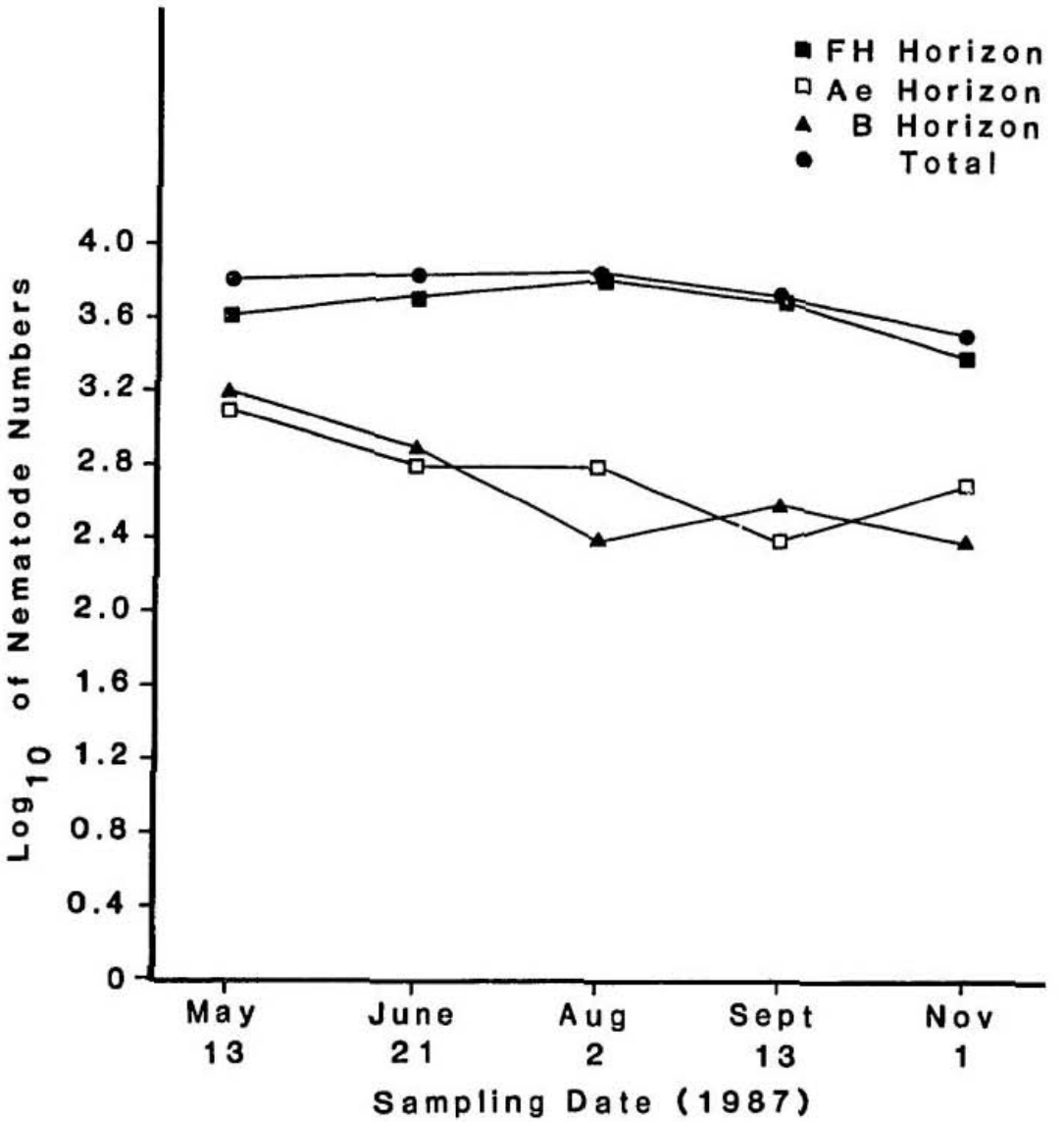

FH Horizon
Ae Horizon
B Horizon
Total
Log10 of Nematode Numbers
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-2: Seasonal changes in the population of nematodes (nematodes/500 c.c. of soil) in the four horizons of the Dryopteris-white birch forest (Site 2) (1987).

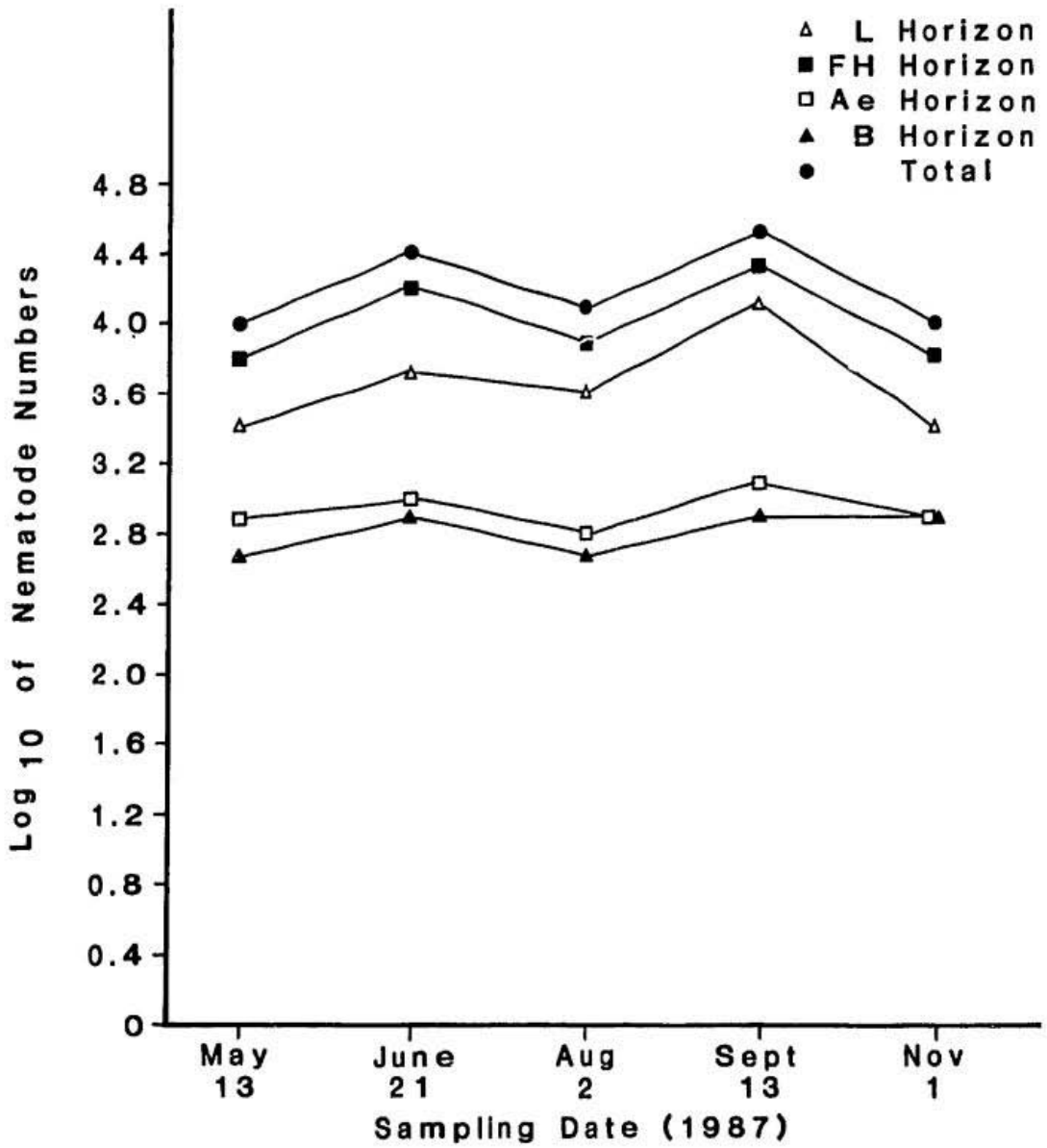

L Horizon
FH Horizon
Ae Horizon
B Horizon
Total
Log 10 of Nematode Numbers
4.8
4.4
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-3: Seasonal changes in the population of nematodes (nematodes/500 c.c. of soil) in the three horizons of the Kalmia heath-barren (Site 3) (1987).

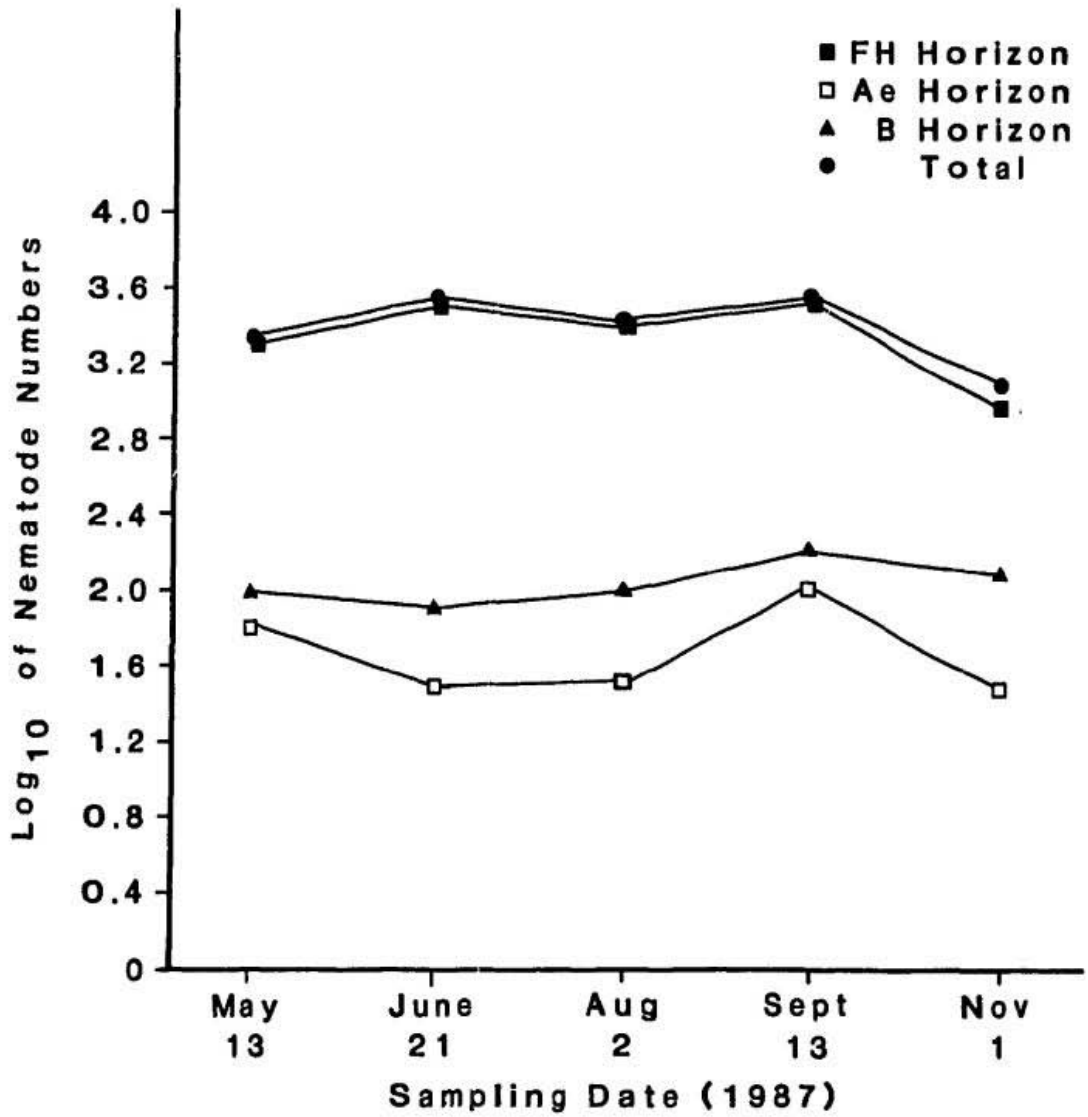

FH Horizon
Ae Horizon
B Horizon
Total
Log10 of Nematode Numbers
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-4: Seasonal changes in the population of nematodes (nematodes/500 c.c. of soil) in the four feeding groups in the three horizons of the black spruce-moss forest (Site 1) (1987).

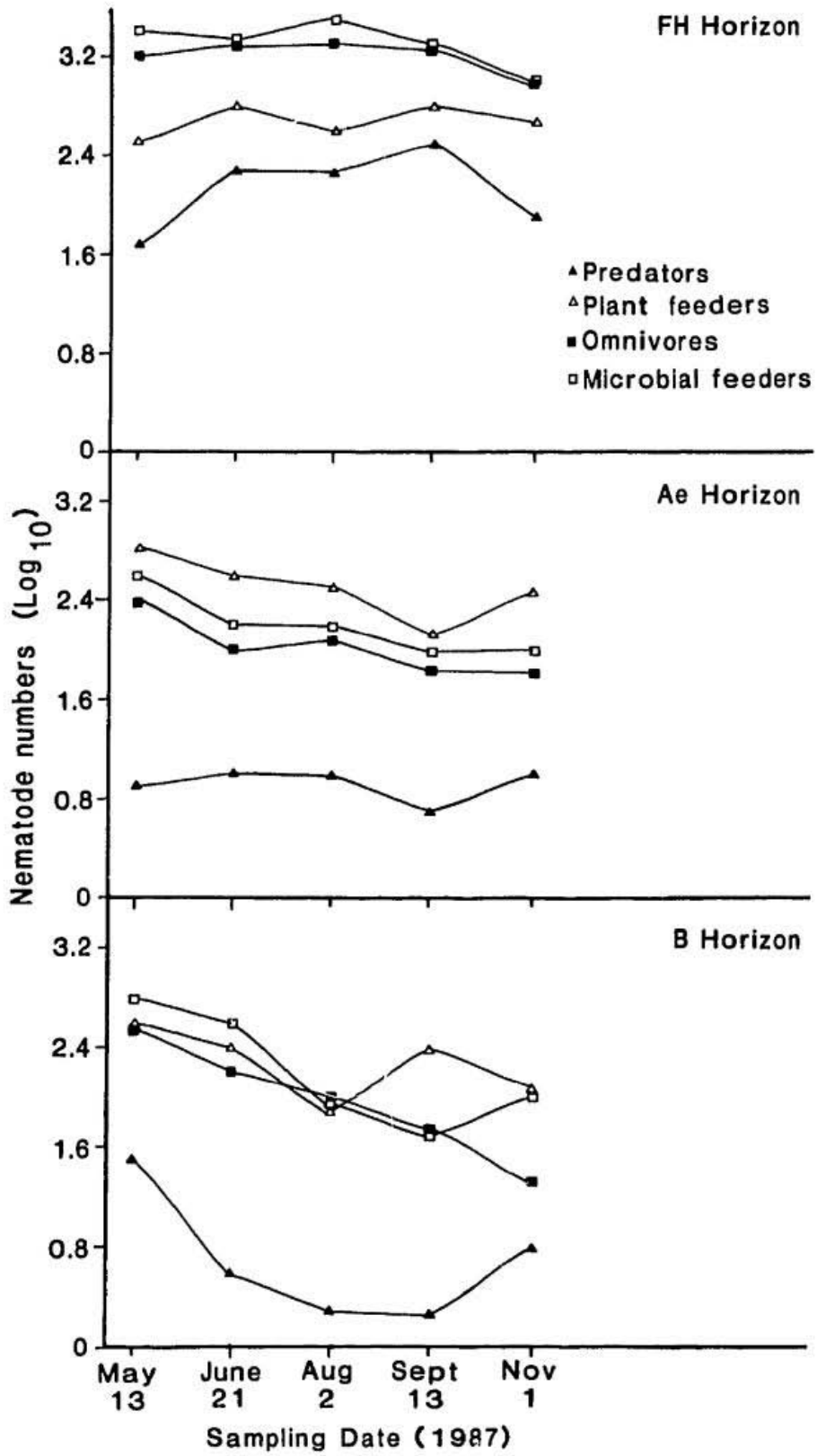

FH Horizon
Ae Horizon
B Horizon
Predators
Plant feeders
Omnivores
Microbial feeders
Nematode numbers (Log 10)
3.2
2.4
1.6
0.8
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-5: Seasonal changes in the population of nematodes (nematodes/500 c.c.of soil) in the four feeding groups in the four horizons of the Dryopteris-white birch forest (Site 2) (1987).

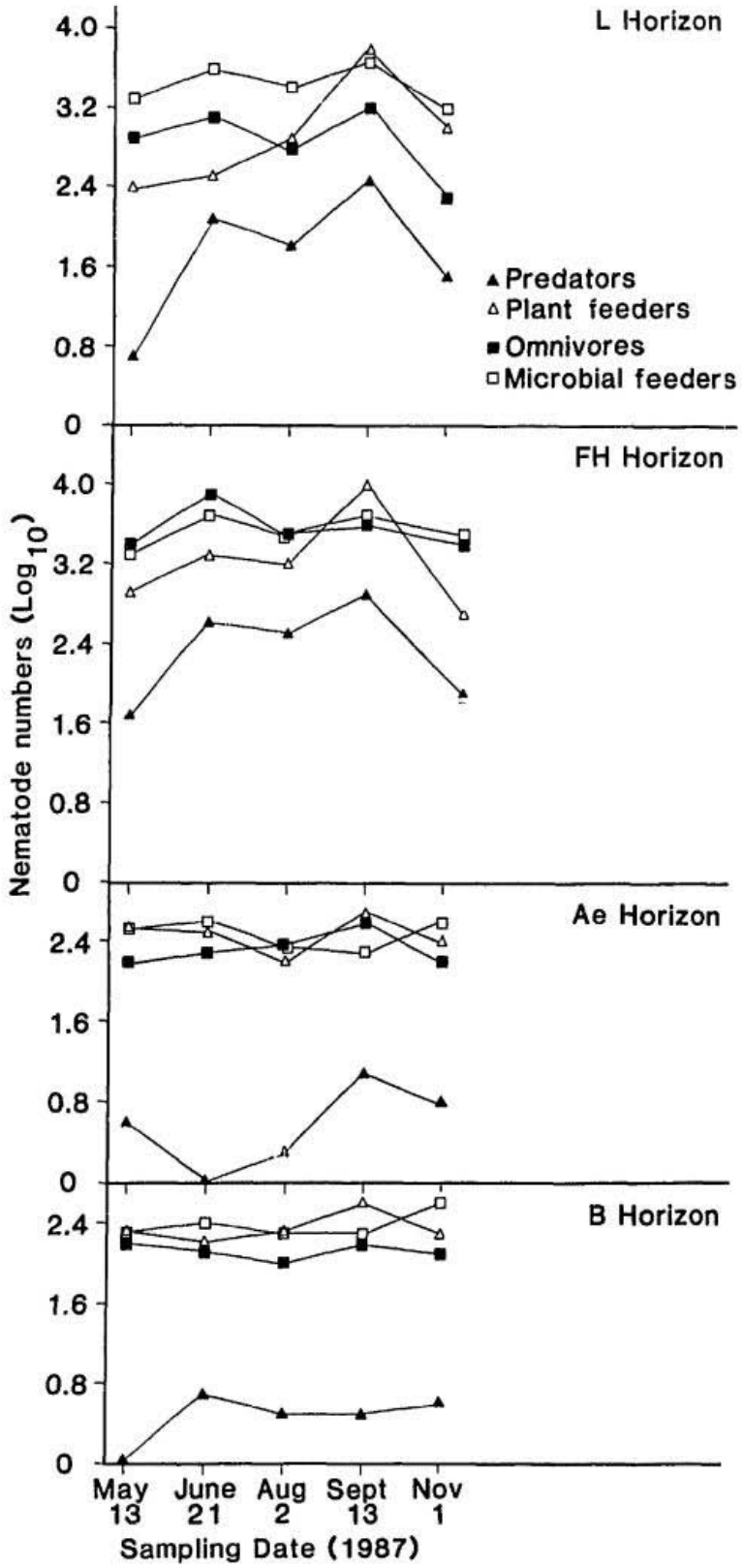

L Horizon
FH Horizon
Ae Horizon
B Horizon
▲ Predators
△ Plant feeders
■ Omnivores
□ Microbial feeders
Nematode numbers (Log10)
4.0
3.2
2.4
1.6
0.8
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-6: Seasonal changes in the population of nematodes (nematodes/500 c.c. of soil) in the four feeding groups in the three horizons of the dry Kalmia heath-barren (Site 3) (1987).

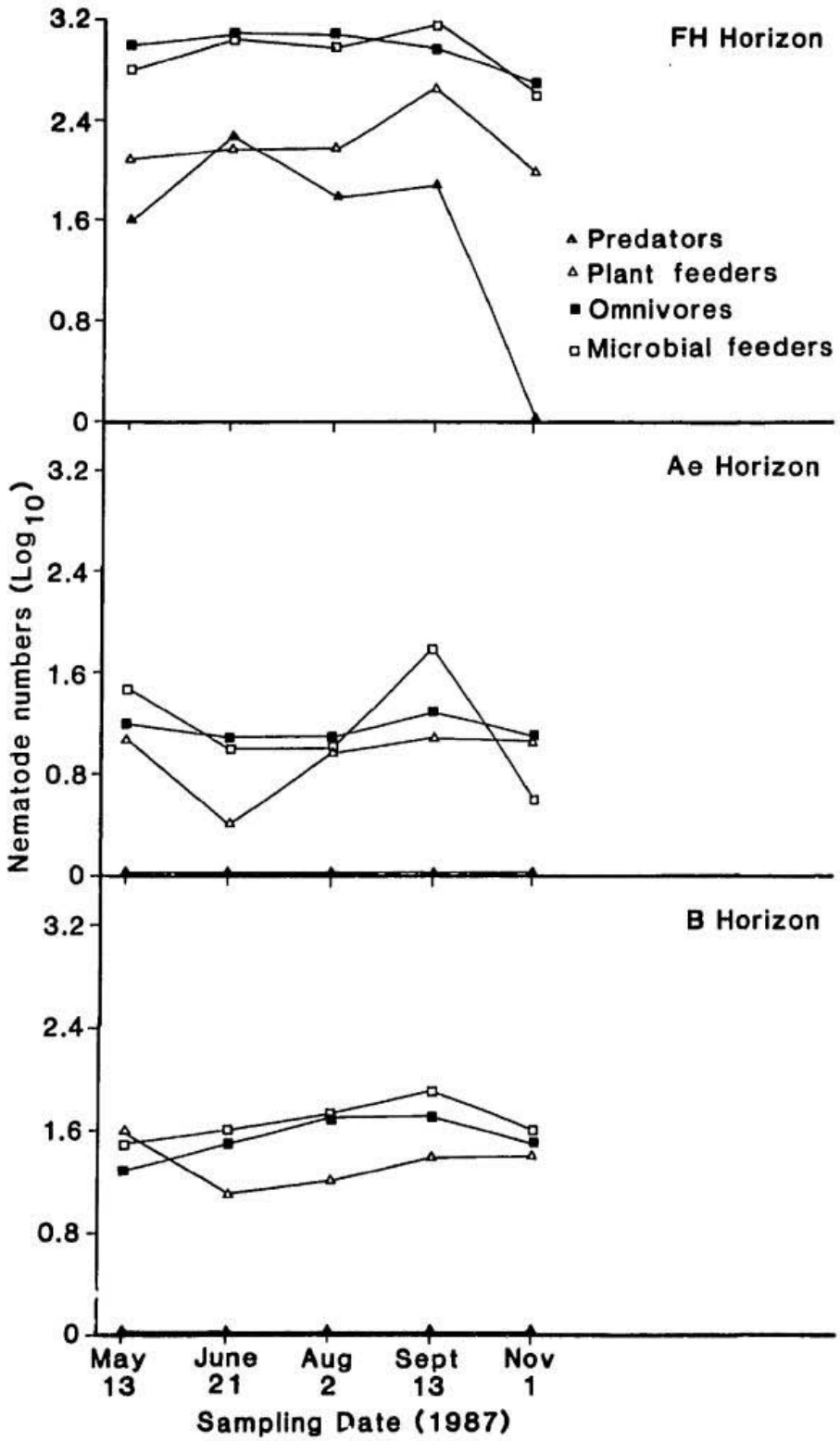

FH Horizon
Ae Horizon
B Horizon
Predators
Plant feeders
Omnivores
Microbial feeders
Nematode numbers (Log10)
3.2
2.4
1.6
0.8
0
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-7: Seasonal changes in the relative importance of the four feeding groups in the three horizons of the black spruce-moss forest (Site 1) (1987).

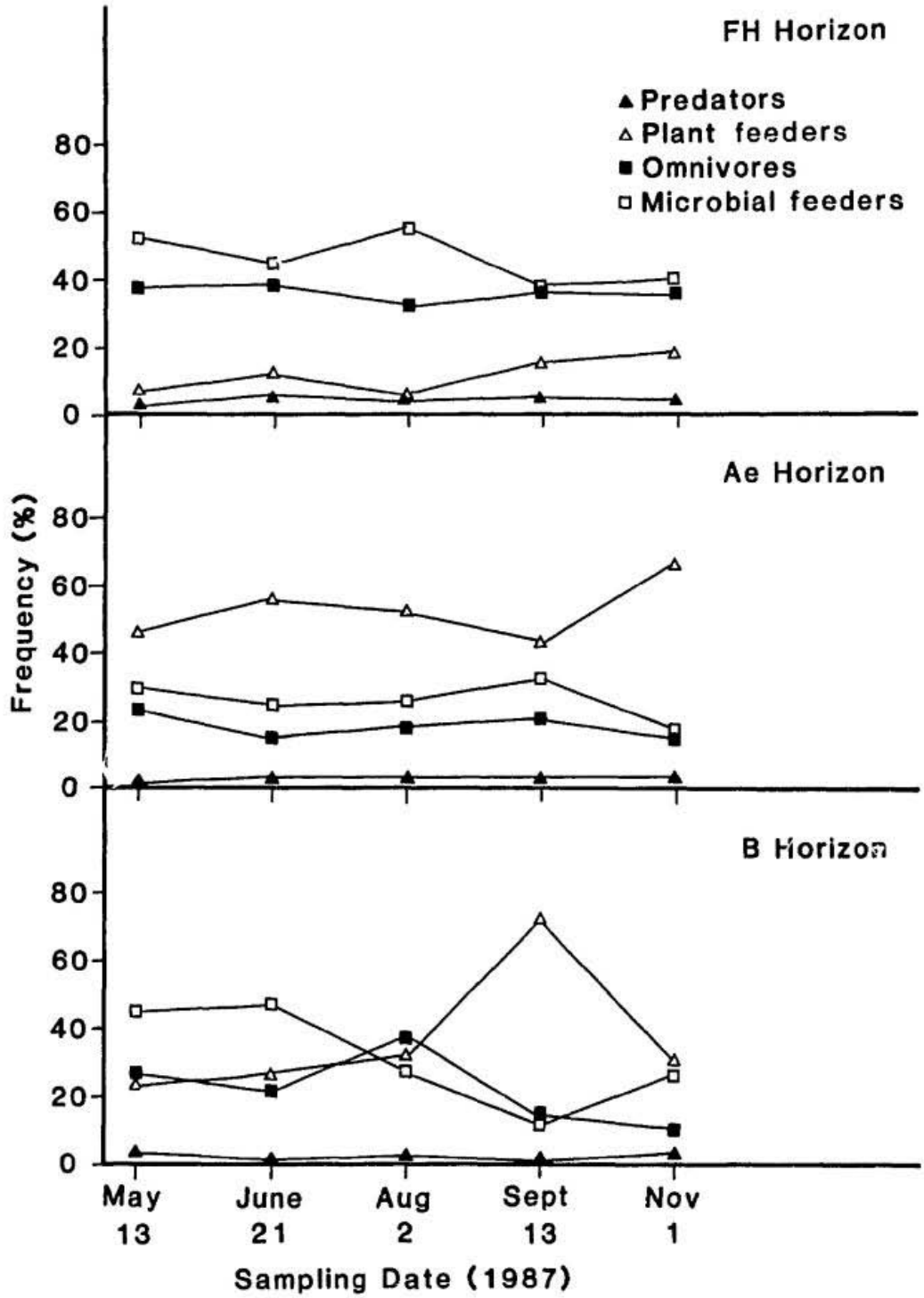

FH Horizon
▲ Predators
△ Plant feeders
■ Omnivores
□ Microbial feeders
Ae Horizon
B Horizon
Frequency (%)
0
20
40
60
80
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-8: Seasonal changes in the relative importance of the four feeding groups in the four horizons of the Dryopteris-white birch forest (Site 2) (1987).

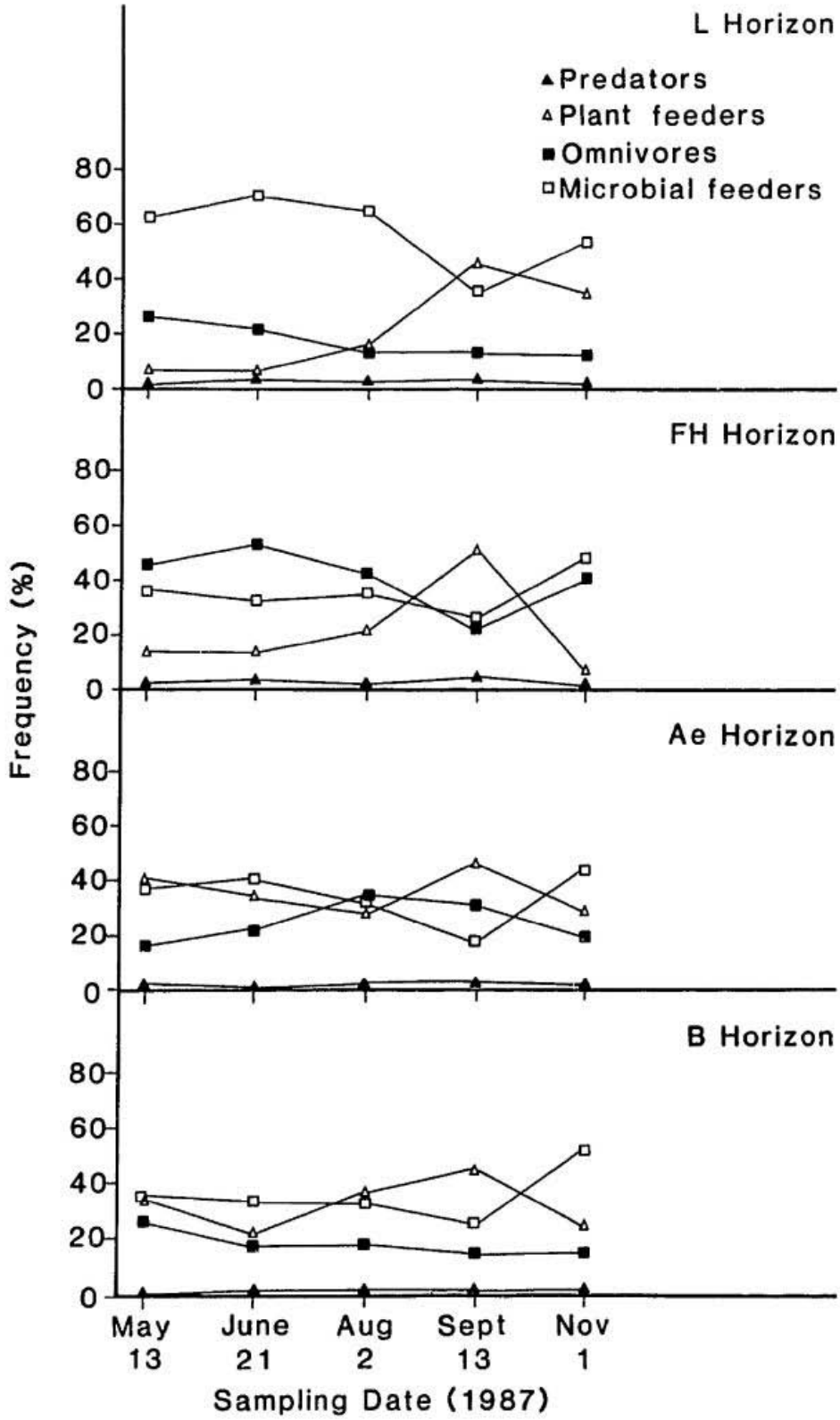
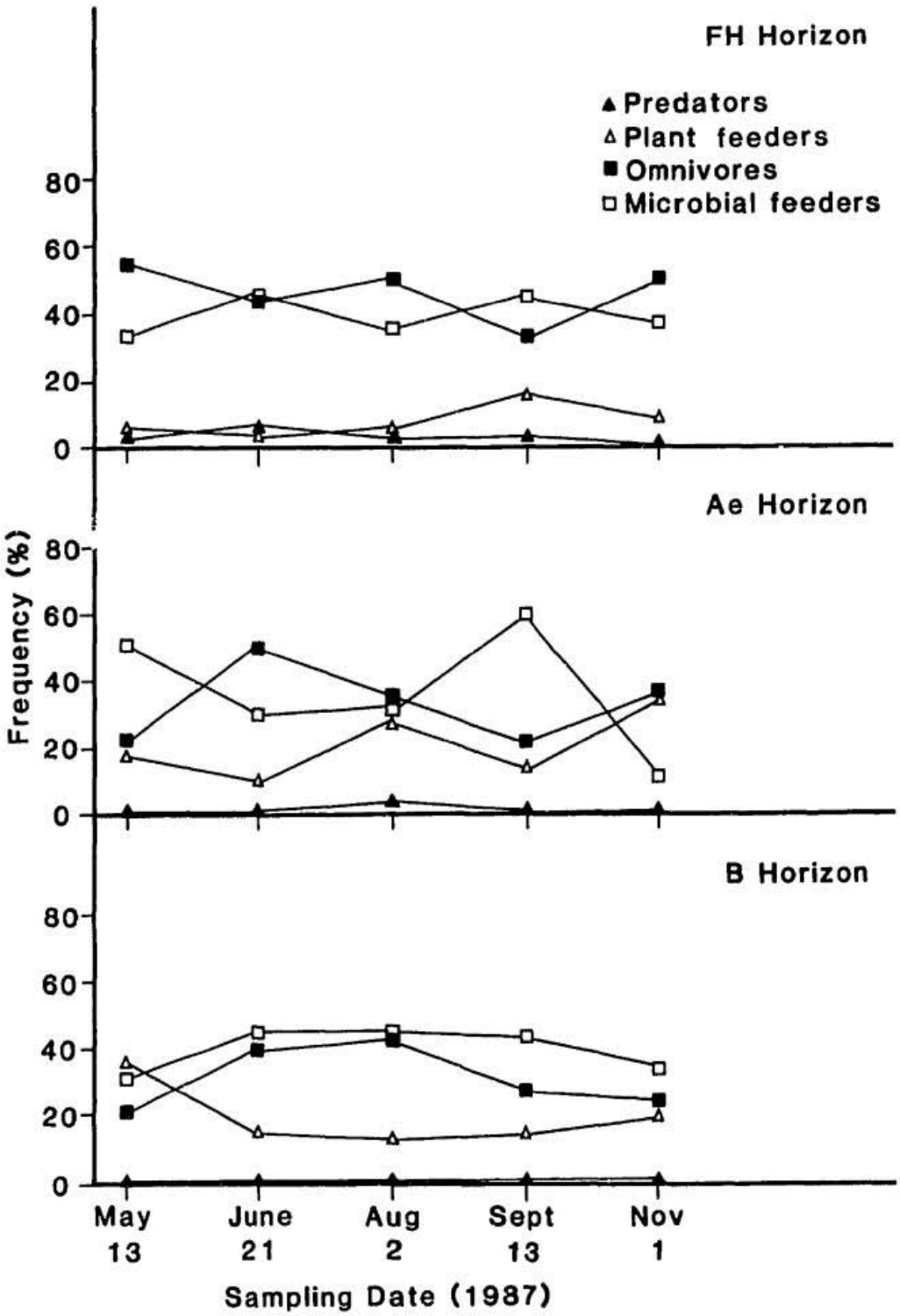

L Horizon
Predators
Plant feeders
Omnivores
Microbial feeders
FH Horizon
Ae Horizon
B Horizon
Frequency (%)
0
20
40
60
80
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

Figure 3-9: Seasonal changes in the relative importance of the four feeding groups in the three horizons of the dry Kalmia heath-barren (Site 3) (1987).


FH Horizon
▲ Predators
△ Plant feeders
■ Omnivores
□ Microbial feeders
Ae Horizon
B Horizon
Frequency (%)
0
20
40
60
80
May 13
June 21
Aug 2
Sept 13
Nov 1
Sampling Date (1987)

1. Populations of nematodes tended to be lower in the dry Kalmia heath-barren.

2. Populations of nematodes in the FH and Ae horizons of the Dryopteris-white birch forest were somewhat higher than those found in the same horizons of the black spruce-moss forest. Within the B horizon, nematode populations were higher in the black spruce-moss forest early in the sampling season, and dropped off over time, while at the Dryopteris-white birch site the populations remained constant over the sampling season. Thus, the end of the season nematode populations were higher in the Dryopteris-white birch forest than in the black spruce-moss forest.

3. The population of nematodes in each of the feeding groups tended to decrease from the FH to the B horizons in the black spruce-moss and Dryopteris-white birch forests at all times. The population of nematodes in the L horizon of the Dryopteris-white birch forest tended to be slightly lower than those found in the FH horizon at this site (in all feeding groups). In the dry Kalmia heath-barren nematode populations in each of the feeding groups tended to be lowest in the Ae horizon.

4. At all sites, layers, and times the population and relative importance of predatory nematodes was very low.

5. Within the FH horizon, at all sites, microbial feeders and omnivores were the feeding groups with the largest populations. These were also the most important component of the nematode fauna in this layer. In the dry Kalmia heath-barren these two groups always made up the bulk of the nematode fauna.

6. Plant feeding nematodes often became a more important component of the nematode fauna in the Ae and B horizons of the two forest habitats. At certain times these became the most important feeding group in this layer. To a lesser extent this was also true of the Kalmia heath-barren.

7. In the one litter layer examined, trends in populations and relative importance of the feeding groups was similar to that of the FH horizons of the black spruce-moss and Dryopteris-white birch forests. However, the population and relative importance of the microbial feeding nematodes was generally greater than that of any other feeding group.

8. In the FH horizons of all sites (and the L horizon of the Dryopteris-white birch site) peak populations of nematodes (in most feeding groups) occurred at the late June and mid-September sampling times. There was no apparent seasonality in the population of nematodes in the Ae and B horizons, with the exception of the B horizon in the black spruce-moss forest. Here, the omnivores decreased over the sampling period and the populations of predatory and microbial feeding nematodes showed distinct drops through the middle of the sampling period.

9. There was an abrupt increase in the population and importance of plant feeding nematodes at the mid-September sampling time, in all layers of the Dryopteris-white birch forest.

3.1. Distribution of Individual Taxa

3.1.1. Predatory nematodes

Prionchulus punctatus (Table 3-2)

Prionchulus punctatus occurred almost exclusively in the black spruce-moss and Dryopteris-white birch forests (it was collected only in September from the FH horizon of the the dry Kalmia heath-barren). It had higher abundances in the FH horizon and L horizons where peaks in abundance were noted at the June and September sampling times.

Mylonchulus brevicaudatus (Table 3-3)

Mylonchulus brevicaudatus occurred in all three sites. This nematode was abundant in the FH horizon but had lower numbers in all other horizons. The seasonal variation in total numbers varied among sites. An August peak in abundance occurred in the black spruce-moss forest. Maximum abundance occurred in mid-September in the Dryopteris-white birch forest, while in the Kalmia heath-barren, abundance peaked in mid-June.

Table 3-2: Vertical and seasonal distribution of abundance of Prionchulus punctatus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	25	127	23	180	-	355
1	Ae	-	3	-	3	-	6
	B	12	-	-	-	-	12
Total		37	130	23	183	-	373
	L	-	124	50	305	24	503
2	FH	28	186	25	78	77	394
	Ae	4	-	-	-	6	10
	B	-	-	-	-	-	-
Total		32	310	75	383	107	907
	FH	-	-	-	6	-	6
3	Ae	-	-	-	-	-	-
	B	-	-	-	-	-	-
Total		-	-	-	6	-	6

Dash indicates the taxon was absent.

Table 3-3: Vertical and seasonal distribution of abundance of Mylonchulus brevicaudatus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	25	83	189	146	89	532
1	Ae	9	8	11	2	9	39
	B	19	4	2	2	7	34
Total		53	95	202	150	105	605
	L	6	-	-	13	62	81
2	FH	17	202	177	705	-	1101
	Ae	-	-	3	13	-	16
	B	-	5	3	3	4	15
Total		23	207	183	734	66	1213
	FH	42	180	60	74	-	356
3	Ae	-	-	1	-	-	1
	B	-	-	-	-	-	-
Total		42	180	61	74	-	357

Dash indicates the taxon was absent.

3.1.2. Plant feeding nematodes

Hirschmanniella sp. was collected only from the litter horizon of the Dryopteris-white birch forest in November (Appendix G). Deladenus sp. occurred sporadically and in low numbers throughout the soil layers of the black spruce-moss and Dryopteris-white birch forests. This species was collected only in May from the FH horizon of the Kalmia heath-barren (Appendix G). Many of the other plant feeding nematodes showed restricted site and vertical distributions.

Two species were largely restricted to the black spruce-moss forest. Neocrossonema menzeli was virtually restricted to this site where it occurred predominantly in the FH horizon (Appendix G). Pratylenchus penetrans occurred mostly in the B soil layer of this site. This species also occurred sporadically, and in low numbers in the Ae and B horizons of the Dryopteris-white birch habitat (Appendix G).

Four plant feeding taxa were largely restricted to the Dryopteris-white birch forest. Three of these, Ecphyadophoridae, Ogma sp., and Nothocriconemella sphagni, were most abundant in the Ae horizon of this site. All three occurred in low numbers in the B horizon, (Ogma sp. and N. sphagni also occurred in the FH layer), of the dry Kalmia heath-barren but were totally absent from the black spruce-moss forest (Appendix G). The fourth, Ditylenchus sp., occurred predominantly in the litter soil layer. Single occurrences of this species were noted in the Ae horizon of the black spruce-moss forest and in the B horizon of the Kalmia heath-barren (Appendix G).

Seriespinula seymouri was virtually restricted to the dry Kalmia heath-barren where it was more abundant in the FH horizon. This species was also recovered in June, from the FH horizon of the black spruce-moss forest (Appendix G).

A brief discussion of the vertical and seasonal distribution of four of the more abundant plant feeding taxa is given below.

Malenchus exiguus (Table 3-4)

This species did not occur in the dry Kalmia heath-barren. Although it did occur consistently in the black spruce-moss forest, its abundance was low (with peaks in the FH horizon in June and mid-September) in this habitat compared to that in the Dryopteris-white birch forest. In this latter habitat highest abundance was attained in the FH and L horizons. A marked peak in abundance was observed in all soil layers at the mid-September sampling time.

Hemicycliophora tenuis (Table 3-5)

Hemicycliophora tenuis occurred in all three sites but abundance was always low in the dry Kalmia heath-barren. Numbers of this species also tended to be low in the Dryopteris-white birch habitat, but there was a single peak in abundance in the Ae soil horizon at the September sampling time. This nematode did not occur in the L horizon of this site. Hemicycliophora tenuis was most abundant in the black spruce-moss forest where maximum abundance occurred in the Ae horizon, but abundance was also relatively high in the B horizon. These

Table 3-4: Vertical and seasonal distribution of abundance of Malenchus exiguus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	54	346	92	346	76	914
1	Ae	-	3	-	-	-	3
	B	12	-	2	-	-	14
Total		66	349	94	346	76	931
	L	153	22	144	5164	32	5515
2	FH	647	977	1491	9494	303	12912
	Ae	11	5	28	229	11	284
	B	47	40	26	241	12	366
Total		858	1044	1689	15128	358	19077
	FH	-	-	-	-	-	-
3	Ae	-	-	-	-	-	-
	B	-	-	-	-	-	-
Total		-	-	-	-	-	-

Dash indicates the taxon was absent.

Table 3-5: Vertical and seasonal distribution of abundance of Hemicycliophora tenuis (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	54	24	80	29	149	336
1	Ae	375	294	230	103	248	1250
	B	138	117	38	162	58	513
	Total	567	435	348	294	455	2099
	L	-	-	-	-	-	-
2	FH	-	-	8	20	-	28
	Ae	25	4	18	169	28	244
	B	31	5	20	7	4	67
	Total	56	9	46	196	32	339
	FH	6	-	-	-	9	15
3	Ae	2	-	4	-	10	16
	B	10	2	-	-	5	17
	Total	18	2	4	-	24	48

Dash indicates the taxon was absent.

two soil layers showed different seasonal patterns of abundance. In the Ae horizon abundance tended to drop off over the summer, and increased again in November. Within the B horizon, however, abundance dropped off over the summer increasing in September, and decreasing again in November.

Aphelenchoides sp. (Table 3-6)

Abundance of Aphelenchoides was generally low in the Kalmia heath-barren. This species occurred sporadically in the Ae and B horizons of this habitat and within the FH horizon peaks in abundance occurred in August and November. Within all the horizons of the black spruce-moss forest abundance maxima of Aphelenchoides sp. were observed in May and August. At this site abundance was highest in the FH horizon.

Within the Dryopteris-white birch forest overall abundance of this nematode remained relatively constant except for increases in September and November. Maximum abundance occurred in the FH and L horizons of this site. Within the FH horizon peaks in abundance occurred in June and September, while in the litter layer abundance increased throughout the sampling period.

Tylenchus sp. (Table 3-7)

In the dry Kalmia heath-barren, abundance of this species was low in the two lower soil layers but was relatively high in the FH horizon, where it attained a maximum in September. In the black spruce-moss forest, patterns of seasonal abundance varied among the soil layers but total abundance remained quite

Table 3-6: Vertical and seasonal distribution of abundance of Aphelenchoides sp. (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	54	34	69	20	47	224
1	Ae	17	3	23	7	2	52
	B	19	4	20	2	2	47
Total		90	41	112	29	51	323
	L	44	39	83	212	270	640
2	FH	38	93	59	98	32	350
	Ae	29	14	15	-	28	86
	B	24	20	26	14	26	110
Total		165	166	183	324	356	1194
	FH	12	14	29	16	36	107
3	Ae	7	-	-	-	-	7
	B	-	-	-	6	2	8
Total		19	14	29	22	38	122

Dash indicates the taxon was absent.

Table 3-7: Vertical and seasonal distribution of abundance of Tylenchus sp. (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	80	102	103	229	178	692
1	Ae	163	68	60	12	79	382
	B	56	59	20	36	53	224
Total		299	229	183	277	310	1298
	L	32	173	-	571	51	847
2	FH	28	976	219	176	174	1573
	Ae	76	70	57	90	133	426
	B	31	60	88	140	132	451
Total		167	1279	364	977	490	3297
	FH	65	97	105	487	42	796
3	Ae	2	3	1	12	-	18
	B	14	5	-	14	5	38
Total		81	105	106	513	47	852

Dash indicates the taxon was absent.

constant throughout the sampling period, with the exception of a slight decrease in the middle of the season. At the Dryopteris-white birch site, total abundance of Tylenchus sp. peaked in June and September. This pattern of seasonal abundance was evident in both the FH and L horizons where abundance of this species was highest. Within the two lower soil layers abundance of Tylenchus sp. tended to increase over the sampling period.

3.1.3. Omnivores

Tylencholaimus nanus, Thonus elegans, and Prodorylaimus sp. occurred sporadically, and in low abundances, throughout the soil layers of all three sites (Appendix G). Aporcelaimellus capitatus also occurred sporadically, and in low numbers, throughout the soil layers of the black spruce-moss and Dryopteris-white birch forests but was absent from the dry Kalmia heath-barren (Appendix G). Paravulvulus planposae occurred in all three sites, but was largely restricted to the FH soil layers (Appendix G). Two omnivorous species that had relatively widespread distributions are discussed separately below.

Diptherophora sp. (Table 3-8)

This species showed low abundance in the dry Kalmia heath-barren. In this habitat, it was largely restricted to the FH horizon, reaching a peak in abundance in August. Within the black spruce-moss forest, abundance was generally highest in the B horizon. At this site, abundance of Diptherophora in all soil layers, tended to be highest at the June and August sampling times.

Highest abundance of this nematode was observed in the Dryopteris-white

Table 3-8: Vertical and seasonal distribution of abundance of Diptherophora sp. (nematodes/500 mls soil) at the three study sites (1087). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	8	10	46	10	24	98
1	Ae	-	27	25	1	17	70
	B	45	80	80	13	2	220
Total		53	117	151	24	43	338
	L	6	-	-	-	-	6
2	FH	51	294	34	372	258	1009
	Ae	22	77	79	205	68	451
	B	8	10	20	14	12	64
Total		87	381	133	591	338	1530
	FH	12	20	55	6	6	99
3	Ae	-	-	2	5	-	7
	B	-	-	-	-	-	-
Total		12	20	57	11	6	106

Dash indicates the taxon was absent.

birch forest where its pattern of vertical distribution differed from that seen in the black spruce-moss forest. Here, abundance was highest in the FH horizon and was generally lower in the Ae and B horizons. This species was virtually absent from the L layer of this site. Within the FH horizon, a peak in abundance of this species was noted in June and a second larger peak in abundance occurred in September. Within the Ae soil layer, numbers of this nematode increased throughout the sampling period, reaching a peak in September, and then showed a marked drop at the November sampling time.

Eudorylaimus carteri (Table 3-9)

This was the most abundant species at all three sites at most sampling times. Highest abundance of this nematode occurred in the Dryopteris-white birch forest. Abundance of E. carteri was consistently much higher in the FH horizon at all three sites.

Seasonal variation of this species varied between the three habitats. Within the black spruce-moss forest total abundance and abundance in the FH layer tended to remain relatively constant during the sampling period but decreased in November. Within the Ae and B horizons abundance was markedly higher at the beginning of the sampling period and tended to decrease thereafter. In the Dryopteris-white birch forest total abundance of E. carteri peaked in June with a lesser peak being observed in September. In the Kalmia heath-barren, however, there was a very clear peak in abundance in the FH horizon at the August sampling time, while in the two lower horizons abundance of this species remained low and relatively constant throughout the sampling period.

Table 3-9: Vertical and seasonal distribution of abundance of Eudorylaimus carteri (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	1534	1820	1763	1901	912	7930
1	Ae	273	73	97	53	47	543
	B	339	67	23	29	18	476
Total		2146	1960	1883	1983	977	8949
	L	799	1123	623	1553	201	4299
2	FH	2372	7641	3395	3700	2199	19308
	Ae	101	136	121	136	57	551
	B	94	90	61	72	81	398
Total		3366	8990	4200	5461	2538	24556
	FH	892	830	1131	781	467	4101
3	Ae	12	10	9	14	12	57
	B	17	30	47	40	27	161
Total		921	870	1187	835	506	4319

3.1.4. Microbial feeding nematodes

Eucephalobus sp. was collected only from the FH horizon of the black spruce-moss forest in June (Appendix G). Micoletzky sp. was collected in November from the FH horizon of this habitat but was also found in June in the FH layer of the dry Kalmia heath-barren, and from both the FH (in May) and B (in September) soil layers of the Dryopteris-white birch stand (Appendix G).

Two species, Achromadora ruricola and Bunonema richtersi, occurred sporadically, and in low numbers, throughout the soil layers of all three sites (Appendix G). Rhabditidae, Teratocephalus sp.1 , and Wilsonema sp. also occurred sporadically in all sites in relatively low numbers, but generally exhibited higher abundances in the L and FH horizons (Appendix G).

Seasonal and vertical distribution of the eight most abundant and widely distributed microbial feeding taxa are discussed below. In general these taxa showed high abundances in the FH horizon, while abundances in the lower (Ae and B) horizons tended to remain low. As discussed under individual taxa, large seasonal variations were seen in the FH horizon, and in some taxa the L horizon. The pattern of seasonal variation in abundances varied among taxa.

Acrobeloides nanus (Table 3-10)

This species was generally abundant at all sites at each of the sampling times. Within the FH horizon of the black spruce-moss forest abundance of A. nanus peaked in September and dropped off markedly at the November sampling

Table 3-10: Vertical and seasonal distribution of abundance of Acrobeloides nanus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	130	195	166	263	66	820
1	Ae	43	31	55	24	52	205
	B	68	184	15	-	51	318
Total		241	410	236	287	169	1343
	L	26	-	54	40	19	139
2	FH	34	93	303	293	258	981
	Ae	69	88	46	73	223	499
	B	71	40	49	61	146	367
Total		200	221	452	467	646	1986
	FH	42	801	407	862	99	2211
3	Ae	10	3	8	19	2	42
	B	14	10	4	18	2	48
Total		66	814	419	899	103	2301

Dash indicates the taxon was absent.

time. In the Ae and B horizons of this site abundance was generally low with the exception of a marked June peak in the B soil layer.

Overall abundance of this nematode in the Dryopteris-white birch habitat, tended to increase over the sampling period. Seasonal patterns of abundance varied greatly among the soil layers. In the FH layer abundance of A. nanus increased to an August maximum and decreased steadily thereafter, while in the Ae and B layers abundance increased sharply at the November sampling time. Within the L horizon abundance of this species was generally low but maxima were observed in the August and September sampling times.

In the dry Kalmia heath-barren abundance of A. nanus was much higher in the FH horizon than in the lower horizons. Overall abundance and abundance in this soil layer showed peaks in June and September.

Teratocephalus sp.2 (Figure 3-11)

This species was most abundant in the FH horizon of all sites and occurred sporadically and in low numbers in the Ae and B horizons. In general this species was more abundant in the Dryopteris-white birch forest. In the FH and L soil layers abundance increased from May to September then showed a decrease in November. In the black spruce-moss forest, overall abundance of Teratocephalus sp.2 and its abundance in the FH horizon showed peaks at the June and September sampling times. This species occurred in low numbers in the Kalmia heath-barren where it was virtually restricted to the FH horizon.

Table 3-11: Vertical and seasonal distribution of abundance of Teratocephalus sp. 2 (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	17	264	92	180	84	637
1	Ae	17	3	-	-	-	20
	B	25	9	2	-	7	43
Total		59	276	94	180	91	700
	L	6	22	29	279	120	456
2	FH	108	108	152	470	355	1193
	Ae	4	-	3	-	8	15
	B	-	5	6	7	4	22
Total		118	135	190	756	487	1686
	FH	24	34	16	16	33	123
3	Ae	-	-	-	2	-	2
	B	-	-	-	-	2	2
Total		24	34	16	18	35	127

Dash indicates the taxon was absent.

Plectus sp. (Table 3-12)

In both the black spruce-moss forest and the dry Kalmia heath-barren, total abundance of Plectus sp. was highest in May. A peak in total abundance was also observed in August. Abundance of this species in the FH horizons of these two sites, showed similar seasonal patterns. Abundance of Plectus sp. in the Ae and B horizons of the black spruce-moss forest tended to decrease throughout the sampling period. Plectus sp. occurred sporadically and in low numbers in the Ae and B horizons of the Kalmia heath-barren.

Total abundance of Plectus sp. in the Dryopteris-white birch forest showed a sharp peak in June, decreased in August, then increased again in September and November. A similar seasonal pattern of abundance of this species was observed in both the FH and Ae horizons of this site. Within the L layer, however, peaks in abundance of Plectus sp. were observed in June and September. Within the B horizon of this site, abundance of this species increased until August and decreased thereafter.

Plectus acuminatus (Table 3-13)

Plectus acuminatus occurred in low numbers in both the black spruce-moss forest and dry Kalmia heath-barren compared to the Dryopteris-white birch forest. In both these habitats abundance of this species was much lower in the Ae and B horizons than in the FH layer. Within the black spruce-moss forest total abundance of P. acuminatus, and its abundance in the FH horizon, tended to

Table 3-12: Vertical and seasonal distribution of abundance of Plectus sp. (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	499	299	710	380	220	2038
1	Ae	154	37	37	7	19	254
	B	426	67	17	11	7	528
Total		1079	333	764	398	246	2820
	L	18	140	70	106	19	353
2	FH	85	1534	615	1096	1070	4400
	Ae	36	1175	57	79	76	1423
	B	47	60	85	68	38	298
Total		186	2909	827	1349	1203	6474
	FH	228	83	100	31	15	457
3	Ae	7	-	1	-	2	10
	B	3	-	6	-	5	14
Total		238	83	107	31	22	481

Dash indicates the taxon was absent.

Table 3-13: Vertical and seasonal distribution of abundance of Plectus acuminatus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	256	244	258	146	207	1111
1	Ae	17	-	7	3	2	29
	B	31	13	-	2	2	48
Total		304	257	265	151	211	1188
	L	1122	1868	1642	2589	685	7906
2	FH	647	976	1062	411	510	3606
	Ae	47	81	46	9	23	206
	B	71	40	26	31	86	254
Total		1887	2965	2776	3040	1303	11972
	FH	147	103	147	195	90	682
3	Ae	17	1	-	12	-	30
	B	10	21	13	4	23	71
Total		174	125	160	211	113	783

Dash indicates the taxon was absent.

decrease until September then increased slightly in November. Within the Kalmia heath-barren, however, total abundance of this species, and its abundance in the FH horizon, tended to increase until September then dropped in November.

Within the Dryopteris-white birch forest the highest numbers of this species were seen in the litter horizon. Both total abundance, and the abundance in this horizon, tended to increase until September then showed a sharp drop in November. Within the FH horizon of this site, numbers of P. acuminatus increased from May to August and decreased throughout the remainder of the sampling period.

Prismatolaimus dolichurus (Table 3-14)

Within the black spruce-moss forest total abundance of this species, and its abundance in the FH horizon, showed maxima in May and August. Abundance tended to decrease throughout the sampling period in the Ae and B horizons of this site. In the FH horizon of the Dryopteris-white birch stand, abundance maxima were seen in June and September, while in the FH soil layer of the Kalmia heath-barren, a large increase in abundance occurred in August and September. Abundance of P. dolichurus in the Ae and B soil layers of the Dryopteris-white birch forest, varied and this nematode was virtually absent from the L horizon of this site. This species occurred sporadically and in low numbers in the Ae and B layers of the Kalmia heath-barren.

Table 3-14: Vertical and seasonal distribution of abundance of Prismatolaimus dolichurus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	596	161	618	254	178	1807
1	Ae	51	68	43	27	-	189
	B	88	59	12	17	22	198
Total		735	288	673	298	200	2194
	L	-	-	8	-	-	8
2	FH	79	388	118	685	129	1399
	Ae	32	41	8	17	17	115
	B	-	35	15	34	17	101
Total		111	464	149	736	163	1623
	FH	81	49	181	189	24	524
3	Ae	-	1	-	16	-	17
	B	3	-	20	16	5	44
Total		84	50	201	221	29	585

Dash indicates the taxon was absent.

Alaimus primitivus (Table 3-15)

Alaimus primitivus occurred sporadically and in low numbers in both the Ae and B horizons of all three sites. Total abundance of Alaimus primitivus in the black spruce-moss habitat, and its abundance in the FH horizon, tended to increase from May to August, dropped in September, and increased again in November. In the FH horizon of the Dryopteris-white birch site there was a large peak in abundance of this species in September, while a peak in abundance was observed in June in the FH horizon of the dry Kalmia heath-barren. Abundance of this nematode in the L horizon of the Dryopteris-white birch forest remained relatively constant throughout the sampling period but was not collected in November from this layer.

Monhysteridae (Table 3-16)

This family, had highest abundance in the L horizon of the Dryopteris-white birch forest. The total abundance in this habitat, and abundance in the L horizon, peaked in June and September. Similar seasonal patterns of abundance of this family were also observed in th Ae and B horizons of this site. Within the FH horizon, however, abundance of this family tended to decrease throughout the sampling period. In the black spruce-moss forest, abundance in the FH horizon increased to an August maximum and then decreased to below initial levels in November. Abundance of Monhysteridae in the lower soil layers of this site tended to decrease throughout the sampling period. Monhysteridae occurred infrequently in the dry Kalmia heath-barren where it occurred almost exclusively in the FH soil horizon.

Table 3-15: Vertical and seasonal distribution of abundance of Alaimus primitivus (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	34	80	29	81	224
1	Ae	-	3	-	10	4	17
	B	6	4	-	-	-	10
Total		6	41	80	39	85	251
	L	18	22	25	27	-	92
2	FH	62	46	59	352	45	564
	Ae	-	-	-	9	6	15
	B	-	-	3	3	4	10
Total		80	68	87	391	55	681
	FH	42	140	76	53	24	335
3	Ae	-	-	-	5	-	5
	B	-	4	1	4	4	31
Total		42	144	77	62	28	353

Dash indicates the taxon was absent.

Table 3-16: Vertical and seasonal distribution of abundance of Monhysteridae (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May	Jun	Aug	Sept	Nov	Total
		13	21	2	13	1	
Site	Layer						
	FH	281	839	933	444	42	2539
1	Ae	60	8	17	19	-	104
	B	-	9	7	2	-	18
Total		341	856	957	465	42	2661
	L	285	1485	813	1447	126	4156
2	FH	602	543	286	352	110	1893
	Ae	7	36	13	26	2	84
	B	8	15	3	3	4	33
Total		902	2079	1115	1828	242	6166
	FH	-	29	16	22	15	82
3	Ae	-	-	-	-	-	--
	B	-	-	-	2	-	2
Total		-	29	16	24	15	84

Dash indicates the taxon was absent.

Eumonhystera sp.(Table 3-17)

Highest abundance of Eumonhystera sp. was observed in the Dryopteris-white birch forest. Within this habitat abundance of this nematode was highest in the FH horizon. A peak in total abundance of Eumonhystera sp. at this site occurred in June and a second increase was noted in September and November. Similar seasonal patterns of abundance of this species were also observed in the L and FH layers of this site. In the black spruce-moss forest abundance maxima were observed in the FH horizon in May and August. Numbers of this species tended to decrease over the sampling period in the Ae and B horizons of this site. Abundance of Eumonhystera sp. was low in the Kalmia heath-barren and this species occurred almost exclusively in the FH horizon.

3.2. Relationship Between Nematode Frequencies and Environmental Variables

Principal Components Analysis of the 11 habitat variables measured in 1986, resulted in the extraction of two principal components (factors) which accounted for 84.2% of the overall variation among the measured variables. Since the subsequent factors had eigenvalues of <1 these were not considered further. Loadings of the 11 environmental variables included on the first two principal components are given in (Table 3-18).

Eight environmental variables had high positive loadings on the first

Table 3-17: Vertical and seasonal distribution of abundance of Eumonhystera sp. (nematodes/500 mls soil) at the three study sites (1987). (Site 1- black spruce-moss forest; Site 2- Dryopteris-white birch forest; Site 3- Kalmia heath-barren)

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	377	151	315	200	126	1169
1	Ae	43	13	6	3	2	67
	B	31	25	10	8	2	76
Total		451	189	331	211	130	1312
	L	70	151	16	173	465	875
2	FH	221	884	286	763	593	2747
	Ae	18	11	10	4	6	49
	B	-	25	9	-	55	89
Total		309	1071	321	940	1119	3760
	FH	30	-	21	31	68	150
3	Ae	-	-	-	-	-	--
	B	-	2	1	-	2	5
Total		30	2	1	31	70	155

Dash indicates the taxon was absent.

Table 3-18: Loadings of environmental variables on the first two factors extracted by Principal Components Analysis.

Environmental Variable	Factor1	Factor2
Available Magnesium	.97527	.12360
Available Potassium	.97147	.12515
Organic Content	.96328	.12198
Available Phosphorus	.95026	.06056
Available Sodium	.94494	.12924
Available Calcium	.91112	.18584
Moisture	.89720	.08315
Available Nitrogen	.85555	.13592
pH	-.77299	-.07441
Temperature	-.09157	.91749
Particle Size	-.43900	-.70926
% Variance explained	72.7	11.5

Principal Component (Factor 1). These were soil moisture, soil organic content, and all the available nutrients (N, P, K, Na, Ca, and Mg). Soil pH, also included in factor 1, had a high negative loading. The two environmental variables with high loadings on the second Principal Component (Factor 2) were soil temperature (a positive loading) and soil particle size (a negative loading).

The stepwise regression analysis is summarized in (Table 3-19). Both derived factors were entered into the analysis. Principal Component 1 accounted for 66% of the variation in nematode numbers and Principal Component 2 accounted for an additional 7% of the variation. Nematode numbers were positively associated with both principal components.

3.3. Nematode Species Assemblages and Relationships with Environmental Factors

Four species occurred in greater than 85% of the samples collected in 1986 and were excluded from the Cluster Analysis: Eudorylaimus carteri, Acrobeloides nanus, Plectus acuminatus and Plectus sp. Also excluded from the analysis were nine species that occurred in less than 5% of samples: Mononchus sp., Hirschmanniella sp., Ogma sp., Eudorylaimus sp., Mesodorylaimus sp., Tylencholaimus sp., Bunonema richtersi, Cephalobus sp. and Euteratocephalus sp..

Results of the Cluster Analysis are summarized in Figure 3-10. When dissimilarity (1/similarity) was plotted against the number of clusters (Figure 3-11) a clear inflection point (indicating an optimum clustering level) occurred at

Table 3-19: Results of Multiple Regression Analysis of mean number of nematodes on the first two principal components extracted from the environmental data.

Step Number	Variable Entered	Equation	R^2	p
1	PC1	y=0.56PC1 + 2.25	.66	<.01
2	PC2	y=0.57PC1 + 0.18PC2 + 2.25	.73	<.01

Figure 3-10: Dendogram showing clustering of samples based on 1986 nematode presence/absence data. (First number in the sample indicates site: 1-black spruce-moss forest, 2-Dryopteris white birch forest, 3-dry Kalmia heath-barren. The second number indicates soil horizon: 1-L, 2-FH, 3-Ae, 4-B. The third number indicates sampling times: 1-May 13, 2-June 21, 3-July 31, 4-Sept. 14, 5-Nov. 2.)

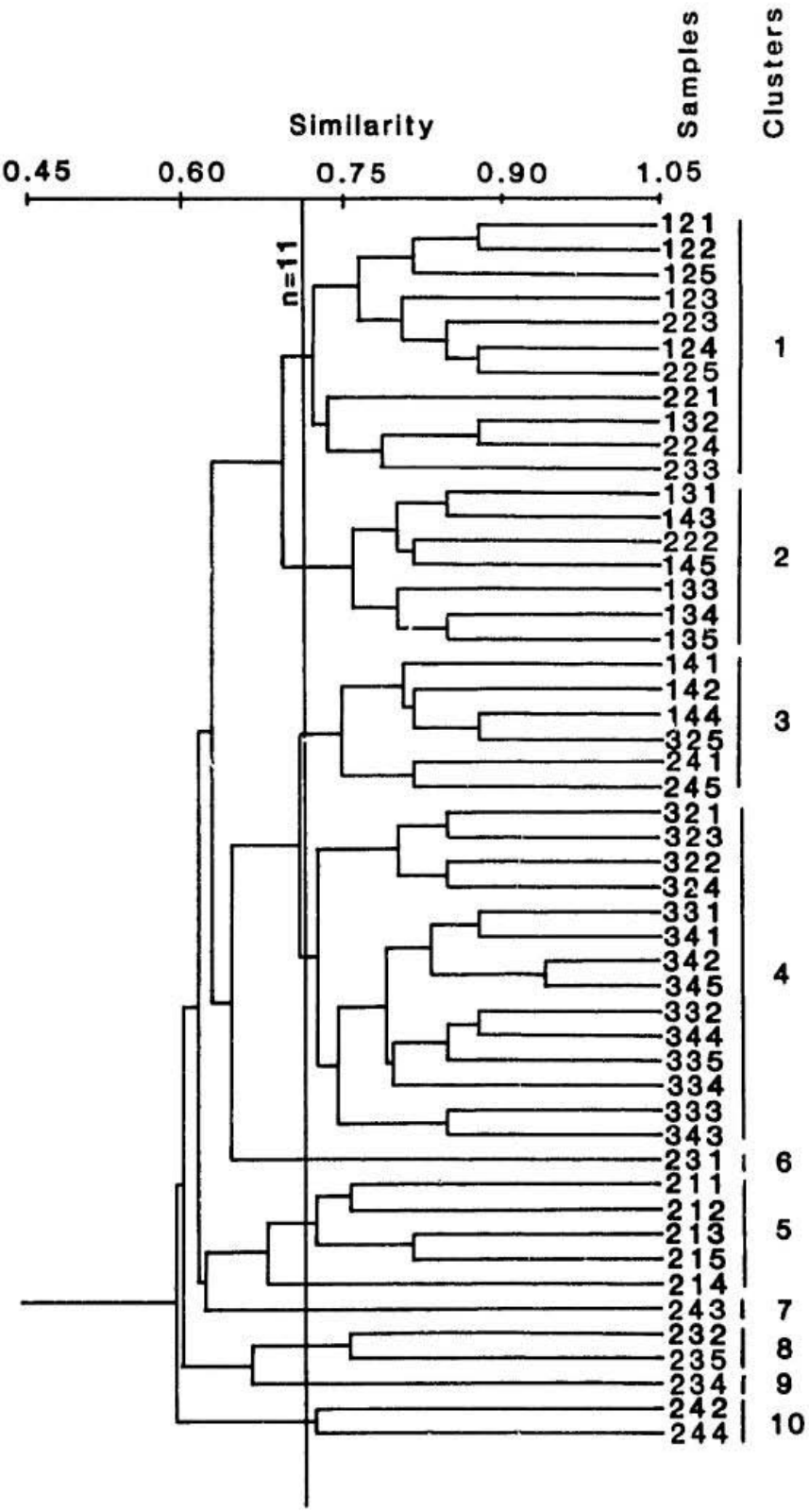
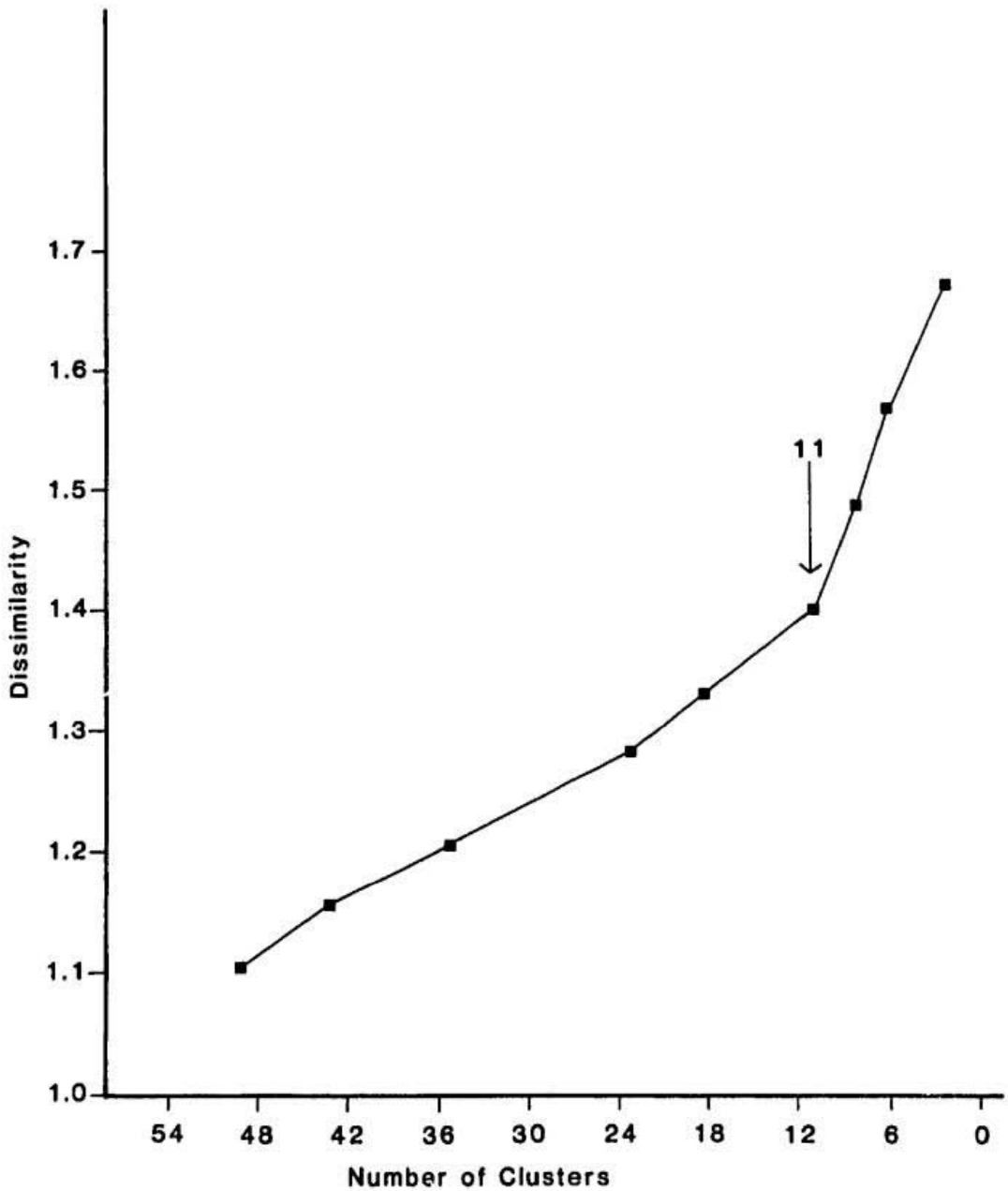

Samples
Clusters
Similarity
0.45
0.60
0.75
0.90
1.05
n=11
121
122
125
123
223
124
225
221
132
224
233
131
143
222
145
133
134
135
141
142
144
325
241
245
321
323
322
324
331
341
342
345
332
344
335
334
333
343
231
211
212
213
215
214
243
232
235
234
242
244
1
2
3
4
6
5
7
8
9
10

Figure 3-11: Plot of dissimilarity against number of clusters for 1986 Cluster Analysis.


Dissimilarity
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
11
54
48
42
36
30
24
18
12
6
0
Number of Clusters

a dissimilarity level of 1.4 with 11 clusters. Even though the analysis indicated that sample 214 should be treated as a separate group, it was included in Cluster 5 since it was from the same site and soil horizon as all other samples in this cluster. Furthermore, the distance between 214 and the rest of Cluster 5 was small. The resulting 10 clusters are indicated on the dendogram (Figure 3-10). Distribution of nematode species among these 10 clusters is given in Table 3-20.

Clusters 6 through 10 were a series of clusters made up of only one or two samples. All samples were from the Ae or B horizons of the Dryopteris white-birch forest. These small clusters were, for the most part, characterized by low species diversity of all feeding groups (Table 3-20). These were not considered further.

Cluster 1 was made up primarily of samples from the felt and humus (FH) horizon of the black spruce-moss, and Dryopteris-white birch forests. The total number of taxa as well as the mean number of taxa per sample, were the highest for all feeding groups except plant feeders (Table 3-20; Table 3-21).

High numbers of microbial feeding nematodes occurred in this cluster compared to clusters 2, 3, and 4 (Table 3-20). Samples making up this cluster also had the highest mean diversity of microbial feeding nematodes (Table 3-21). Although the number of plant feeding nematodes found in the cluster as a whole is high (10), the mean number per sample was only 3.7 (Table 3-21).

The predatory nematode, Mylonchulus brevicaudatus, and the microbial feeding nematodes Alaimus primitivus, Prismatolaimus dolichurus and

Table 3-20: Distribution of the 33 nematode taxa among the 10 groups resulting from Cluster Analysis. (+ indicates taxon present, - indicates taxon absent)

	Cluster Number									
	1	2	3	4	5	6	7	8	9	10
Taxa										
Predators										
Mylonchulus brevicaudatus	+	+	+	+	+	-	+	+	-	+
Prionchulus punctatus	+	+	-	+	+	-	+	-	-	-
Plant feeders										
Aphelenchoides sp.	+	+	+	+	+	-	+	+	-	+
Coslenchus costatus	+	+	-	+	-	-	-	-	-	-
Deladenus sp.	+	+	+	-	+	-	-	+	-	-
Ditylenchus sp.	-	+	-	-	+	-	-	+	-	-
Ecphyadophoridae	+	-	-	+	-	+	-	+	+	-
Hemicycliophora tenuis	+	+	+	+	-	+	-	+	-	-
Malenchus exiguus	+	+	+	+	+	-	+	+	+	+
Neocrossonema menzeli	+	+	+	-	-	-	-	-	-	-
Nothocriconemella sphagni	+	+	-	+	+	+	-	+	+	+
Pratylenchus penetrans	+	+	+	-	-	-	-	-	+	+
Seriespinula seymouri	-	-	+	+	-	-	-	-	-	-
Tylenchus sp.	+	+	+	+	+	+	+	+	+	+
Omnivores										
Aporcelaimellus capitatus	-	-	+	-	-	-	+	-	+	-
Diptherophora sp.	+	+	+	+	+	+	-	+	+	+
Paravulvulus planposae	+	+	-	+	+	-	+	+	+	+
Prodorylaimus sp.	-	-	-	+	-	+	+	-	-	-
Thonus elegans	+	+	+	+	-	-	-	+	+	+
Tylencholaimus nanus	+	+	-	-	-	-	-	+	-	+

Table 3-20 continued_

	Cluster Number									
	1	2	3	4	5	6	7	8	9	10
Microbial feeders										
Achromadora ruricola	+	-	+	+	+	+	-	+	-	..
Alaimus primitivus	+	+	+	+	+	-	+	+	-	-
Eucephalobus sp.	+	+	-	+	-	-	+	-	-	-
Eumonhystera sp.	+	-	+	-	+	+	-	+	-	-
Micoletzky sp.	+	-	-	-	+	-	-	-	-	-
Monhysteridae	+	+	+	-	+	-	+	+	+	+
Prismatolaimus dolichurus	+	+	+	+	+	-	+	+	+	-
Rhabditidae	+	+	-	-	+	-	-	+	+	-
Teratocephalus sp1.	+	-	-	+	+	-	+	-	-	+
Teratocephalus sp2.	+	-	+	+	+	-	-	+	+	-
Wilsonema sp.	+	-	-	+	+	-	-	-	-	+
Unknowns										
Unidentified A	+	-	-	+	-	+	-	+	+	+
Unidentified B	+	-	+	-	-	+	+	-	-	+
Predators	02	02	01	02	02	00	02	01	00	01
Plant feeders	10	10	08	08	06	04	03	08	05	05
Omnivores	04	04	03	04	02	02	03	04	04	04
Microbial feeders	11	05	06	07	10	02	05	07	03	03
Unknowns	02	00	01	01	00	02	01	01	01	02
Total Taxa	29	21	19	22	20	10	14	21	14	15

Table 3-21: Mean diversity of nematode taxa from 4 feeding groups in samples of the five major groups resulting from Cluster Analysis.

	Cluster Number				
	1	2	3	4	5
Feeding Group					
Predators	1.6	1.0	0.5	0.5	1.0
Plant feeders	3.7	5.0	4.0	3.1	3.6
Omnivores	2.4	2.3	1.8	1.2	0.4
Microbial feeders	6.2	3.0	2.7	1.9	4.2
Total	14.1	11.3	9.2	7.1	9.2

Eumonhystera sp., occurred in all the samples of Cluster 1 (Table 3-22). Alaimus primitivus had high constancies in clusters 1 and 2 but low constancies in the other clusters while Eumonhystera sp. had high constancy in Cluster 1 and low constancies in all other clusters (Table 3-22). Only four taxa, two plant feeders and two omnivores, were completely absent from this cluster.

Cluster 2 was largely composed of samples from the Ae horizon of the black spruce-moss forest, but also included some samples of the B horizon from this site. The total number of taxa that occurred in this cluster was high for all feeding groups, with the exception of the microbial feeding nematodes (Table 3-20). This pattern of overall diversity was reflected in the individual samples; the mean number of taxa in samples of this group was second only to that found in Cluster 1 (Table 3-21). Individual samples of this cluster showed the highest mean diversity of plant feeding nematodes among all clusters (Table 3-21).

Three species occurred in all samples of Cluster 2: Hemicycliophora tenuis, a plant feeder; Diptherophora sp., an omnivore; and Alaimus primitivus, a microbial feeder (Table 3-22). Pratylenchus penetrans, a plant feeder, had low constancy in all other clusters but had a high constancy in this cluster (Table 3-22). Twelve taxa were absent from all the samples of this cluster. Six of these were microbial feeders (Table 3-20). Two of these microbials feeders, Achromadora ruricola and Teratocephalus sp.2, were absent only from this cluster (Table 3-22).

Cluster 3 was composed primarily of samples from the B horizon of the black spruce-moss, and Dryopteris white birch forests. This cluster as a whole

Table 3-22: *Constancies of 33 nematode taxa in the five major groups identified by Cluster Analysis. Constancies are expressed as the percentage of samples (rounded to nearest 1%) from each cluster in which the species occurred (dash indicates taxon absent).*

	Cluster Number				
	1	2	3	4	5
Number of samples/cluster	11	7	6	14	5
Taxa					
Predators					
Mylonchulus brevicaudatus	100	86	50	43	20
Prionchulus punctatus	64	14	-	7	80
Plant feeders					
Aphelenchoides sp.	36	43	83	57	80
Coslenchus costatus	9	14	17	7	-
Deladenus sp.	9	29	-	-	60
Ditylenchus sp.	-	14	-	-	60
Ecphyadophoridae	9	-	-	7	-
Hemicycliophora tenuis	64	100	83	71	-
Malenchus exiguus	91	86	29	14	60
Neocrossonema menzeli	46	43	17	-	-
Nothocriconemella sphagni	36	14	-	14	20
Pratylenchus penetrans	9	86	50	-	-
Seriespinula seymouri	-	-	17	64	-
Tylenchus sp.	64	71	100	79	80
Omnivores					
Aporcelaimellus capitatus	-	-	50	-	-
Diptherophora sp.	91	100	100	36	20
Paravulvulus planposae	91	71	-	43	20

Table 3-22 continued

	Cluster Number				
	1	2	3	4	5
Number of samples/cluster	11	7	6	14	5
Prodorylaimus sp.	-	-	-	7	-
Thonus elegans	45	43	29	36	-
Tylencholaimus nanus	9	14	-	-	-
Microbial feeders					
Achromadora ruricola	18	-	17	50	20
Alaimus primitivus	100	100	17	29	40
Eucephalobus sp.	9	14	-	7	-
Eumonhystera sp.	100	-	17	-	40
Micoletzky sp.	18	-	-	-	20
Monhysteridae	82	57	50	-	100
Prismatolaimus dolichurus	100	86	83	71	40
Rhabditidae	64	43	-	-	60
Teratocephalus sp1.	9	-	-	7	20
Teratocephalus sp2.	91	-	83	14	20
Wilsonema sp.	36	-	-	7	60
Unknowns					
Unidentified A	9	-	-	43	-
Unidentified B	9	-	17	-	-

showed intermediate numbers of nematodes in all feeding groups (Table 3-20). This pattern was also apparent in the individual samples making up this cluster (Table 3-21).

The plant feeder Tylenchus sp., and the omnivore Diptherophora sp. occurred in all samples of this cluster (Table 3-22). Aporcelaimellus capitatus, an omnivore, occurred only in samples of this cluster but did not show a particularly high constancy (Table 3-22). Nothocriconemella sphagni (plant feeder) and P. avulvulus planposae (omnivore), two species which occurred in all of the other clusters, were absent from Cluster 3. In addition, the family Rhabditidae, (composed of omnivores), was absent from this and Cluster 4 (Table 3-22).

Cluster 4 included only samples from the dry Kalmia heath-barren and all but one of the samples collected from this site were included in this cluster. Although the total number of nematode taxa in this cluster from each of the feeding groups ranged between 2 and 8 (Table 3-20), nematode diversity in individual samples was the lowest of all the clusters (Table 3-21). This was particularly true of the plant feeding nematodes. The total number in the cluster was high (8), but the mean number found within a sample was the lowest of any cluster (only 3.1) (Table 3-21). A similar pattern was exhibited by the omnivorous and microbial feeding taxa. Four omnivorous and seven microbial feeding taxa occurred in the cluster as a whole, while individual samples showed mean numbers of 1.2 and 3.4 taxa (respectively).

Cluster 4 was characterized by low constancies of most taxa which were

present (Table 3-22). Achromadora ruricola, a microbial feeder, and Seriespinula seymouri, a plant feeder, showed intermediate constancies within this cluster but showed low constancies in all other clusters (Table 3-22). The family Monhysteridae was absent only from this cluster (Table 3-22).

Cluster 5 was composed entirely of samples collected from the litter horizon of the Dryopteris white birch forest. This cluster showed low diversity of plant feeders and omnivores, but was rich in microbial feeding taxa (Table 3-20). Although the total number of plant feeding taxa was low in the cluster as a whole, the diversity of plant feeders per sample was similar to that found in clusters 1 and 3 (Table 3-21). The diversity of omnivores per sample was extremely low; this group was absent from 3 of the 5 samples and the remaining two each had a single taxon (Table 3-21). The high diversity of microbial feeding taxa found in this cluster was reflected in the mean number of microbial feeding taxa per sample (Table 3-21).

The family Monhysteridae (microbial feeders), was present in all the samples of Cluster 5. Four species had fairly high constancies within this cluster but had much lower constancies in all other clusters: Prionchulus punctatus (predator), Deladenus sp. (plant feeder), Ditylenchus sp. (plant feeder) and Wilsonema sp. (microbial feeder) (Table 3-22). The microbial feeder Prismatolaimus dolichurus had low constancy within this cluster but had much higher constancies in all other clusters (Table 3-22). Thonus elegans, an omnivore, and Hemicycliophora tenuis, a plant feeder, absent from Cluster 5, had intermediate to high constancies in all other clusters (Table 3-22).

3.3.1. Discriminant functions analysis

The transformed means and standard deviations of each of the 10 environmental variables included in the analysis, are given for each cluster in Table 3-23. Two significant discriminant functions, accounting for 83.6% of the among cluster variation, were extracted from the environmental data matrix (Table 3-24). The separation of the five clusters on these two discriminant axes is shown in Figure 3-12.

Discriminant Function 1 loaded heavily on available K and N (negatively) and on pH, available P, and moisture (positively) (Table 3-24). Cluster 4 separated from all other clusters on the basis of this function. Discriminant Function 2 had high loadings on available Mg and organic content (positive) as well as on available Na, Ca and soil moisture (negative) (Table 3-24). Cluster 5 separated from all other clusters on this function.

The discriminant functions were successful in their ability to correctly assign samples to clusters on the basis of the environmental characteristics; approximately 88% of the 43 samples used in the analysis were correctly assigned (Table 3-25). One hundred per cent classification was achieved for Cluster 5. Only a single sample from each of clusters 1, 3, and 4 was incorrectly assigned. The least successful classification was obtained for Cluster 2 which had two of five samples incorrectly assigned.

Table 3-23: Means and standard deviations of the 10 measured soil variables for each of the five major groups identified by Cluster Analysis. Values given are log-transformed, except organic content and particle size which are arcsine-transformed. Values in parentheses are standard deviations.

	Cluster				
	1	2	3	4	5
Variable					
pH	3.70 (0.20)	4.26 (0.37)	4.50 (0.49)	4.38 (0.50)	3.90 (0.31)
% Organic content	0.87 (0.34)	0.35 (0.35)	0.40 (0.15)	0.43 (0.34)	1.18 (0.16)
Available N	1.97 (0.70)	0.99 (0.83)	1.22 (0.32)	0.86 (0.49)	2.48 (0.42)
Available P	0.46 (0.55)	0.66 (0.60)	0.44 (0.43)	0.82 (0.47)	2.11 (0.15)
Available K	2.62 (0.60)	1.64 (0.61)	1.64 (0.40)	1.57 (0.63)	3.00 (0.16)
Available Na	1.89 (0.38)	1.27 (0.37)	1.31 (0.29)	1.29 (0.56)	1.93 (0.16)
Available Ca	2.66 (0.65)	1.21 (0.98)	0.68 (1.15)	1.53 (1.09)	3.37 (0.16)

Table 3-23 continued_

	Cluster				
	1	2	3	4	5
Variable					
Available Mg	2.53	1.48	1.42	1.67	3.08
	(0.56)	(0.64)	(0.63)	(0.82)	(0.14)
Moisture	0.30	-0.31	-0.19	-0.18	0.18
content	(0.39)	(0.31)	(0.29)	(0.40)	(0.26)
Particle size	0.52	0.70	0.64	0.59	0.52
(% soil > 2mm)	(0.10)	(0.11)	(0.03)	(0.09)	(0.15)

Table 3-24: Summary of Discriminant Functions Analysis on environmental data for the five groups of samples identified by Cluster Analysis.

	Function No.	
	1	2
Percent of among-cluster variation accounted for	49.4	34.2
Cumulative percent of variance accounted for	49.4	83.6
Microhabitat variables and DF coefficients		
Available K	-2.900	-0.052
Available N	-1.315	-0.032
Available P	1.116	-1.045
Available Mg	0.442	5.304
Available Na	0.778	-3.139
Available Ca	0.687	-1.190
pH	0.964	0.844
Organic content	0.318	2.053
Moisture content	1.532	-1.580
Particle size	-0.534	0.189

Figure 3-12: Separation of five clusters on the first two discriminant axes.

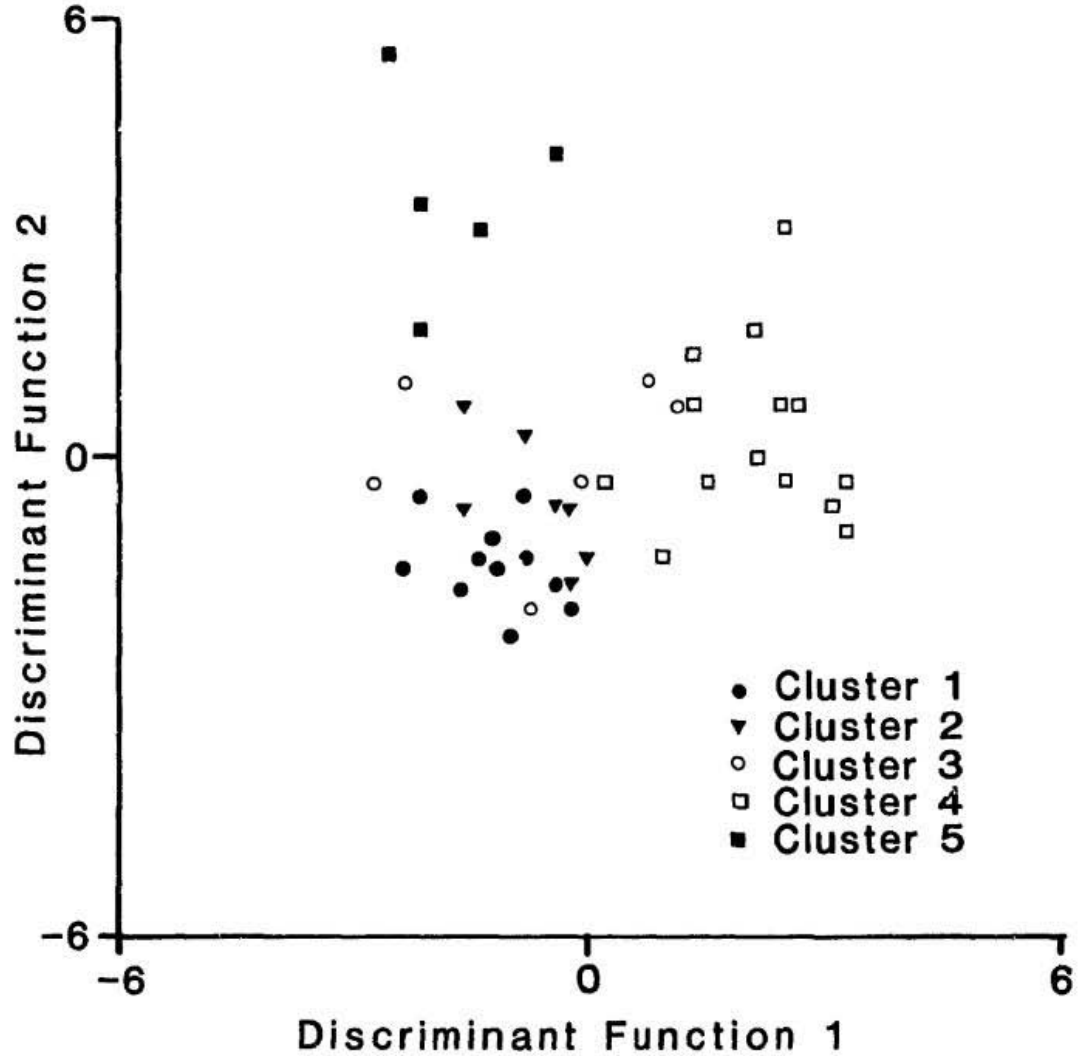

6
0
-6
-6
0
6
Discriminant Function 2
Discriminant Function 1
Cluster 1
Cluster 2
Cluster 3
Cluster 4
Cluster 5

Table 3-25: Discriminant Functions Classification of the five clusters. Numbers in parentheses are percentages.

	Predicted Cluster Membership				
	1	2	3	4	5
Actual Cluster Number					
1	10 (90.9)	1 (9.1)	0 —	0 —	0 —
2	1 (14.3)	5 (71.4)	1 (14.3)	0 —	0 —
3	0 —	1 (16.7)	5 (83.3)	0 —	0 —
4	1 (7.1)	0 —	0 —	13 (92.9)	0 —
5	0 -	0 -	0 -	0 -	5 (100)

Overall Classification Success = 88%

Chapter 4

DISCUSSION

A total of 46 nematode taxa, from 7 orders, were collected from the three study sites: 36 occurred in the black spruce-moss forest, 41 in the Dryopteris-white birch forest, and 37 in the dry Kalmia heath-barren. All taxa collected are widely distributed in the temperate and boreal zones. Although no new species were identified this does not imply that none were present. Further work on taxa not identified to species level is needed to establish if indeed any new species existed.

No studies from boreal areas exist to which the present work can be directly compared. There are, however, several studies from temperate and Arctic regions. In temperate regions, totals of 62-228 nematode species have been reported from sites which include a number of hardwood and mixed-forest habitats (Bassus, 1962; Yuen, 1966; Johnson et al., 1972; Yeates, 1972; Popovici, 1980), as well as several grassland types (Yuen, 1966; Orr and Dickerson, 1967; Yeates, 1974). Species diversities in Arctic locations are also higher than the diversity encountered in the present study; 89 species from 45 genera were reported from Spitzbergen (Loof, 1971 in Spaull, 1973b), and 75 species from 40 genera have been reported from a variety of studies on Ellesmere Island (Spaull, 1973b).

Direct comparison of the present work with any of the above studies may be inappropriate since, generally, a greater variety of habitats were examined in the latter. This may have increased the diversity of nematodes encountered. Species numbers similar to those encountered in this study have been reported for some specialized habitats in otherwise temperate areas. For example, Yeates (1967) reported 59 nematode species from 6 sand dune habitats in New Zealand, while Banage (1966) found 38 genera in acidic moorland soils in England. Low diversity in the moorland sites was attributed to the acidity of the soil, and this may also be a factor contributing to lower diversity in the present study where pH ranged from 3.4 to 5.1.

The results of the Principal Components Analysis reveal that organic content, soil moisture, and all available soil nutrients (positive loadings) can be grouped, along with pH (negative loading), as a single factor influencing nematode abundance. The basis of this component or factor appears to largely reflect high levels of organic matter and associated high levels of available nutrients or, more simply, high soil productivity. High positive loading of soil moisture on the same axis may reflect the increased water retentive ability of those soils with high organic content. Since decomposition of organic matter results in more acidic soils it is not surprising that pH has a negative loading on this factor.

From the results of the Regression Analysis it is evident that soil productivity (as indicated by organic content and nutrient availability) is the main factor governing nematode populations in this study. Soil productivity is likely to directly affect nematode numbers by its effects on food supply for all

nematode trophic groups. Higher soil productivity results in an increase in other soil faunas, bacteria, fungi, algae, and plant roots. Other researchers have recognized that food availability is a factor governing nematode abundance (Nielsen, 1949; Bunt, 1954; Egunjobi, 1968). Positive relationships documented between nematode numbers and increased humus content and/or plant cover (Wasilewska, 1971; Kuzmin, 1976) may also reflect overall soil productivity.

The Principal Components and Regression analyses reveal a second grouping of environmental variables that also correlate with nematode abundance in this study, but to a much lesser degree than soil productivity. This second factor is a function of soil temperature (positive loading) and soil particle size (negative loading). The relationship between temperature and particle size is not clear. It is possible that they merely reflect increasing depth, since temperature is negatively correlated, and particle size positively correlated, with increasing soil depth. Both temperature and particle size have been shown to affect nematode abundance.

Temperature exerts direct effects on the physiology of nematodes. Optimal temperature range varies between nematode species, with some preferring warmer, and others cooler temperatures (Norton et al., 1971). In addition, any given species activity such as egg hatching, reproduction, movement, and development, will have different temperature requirements. In this study low rather than high temperatures are more likely to limit nematode populations.

The relationship between nematodes and soil particle size has been discussed

in detail by Wallace (1958), Jones and Thomasson (1976), and Norton (1979). Particle size affects the space available to nematodes by its direct effects on pore space. When pore diameter is less than the diameter of the average nematode (approximately 30 μm, (Jones and Thomasson, 1976)) the spaces are obviously unusable. When pores are large, however, much of the space may still be unusable to nematodes for three reasons:

- a) Nematodes require a continuous liquid film for movement. Larger pores are often air filled, and thus the surface area usable by nematodes is reduced.
- b) In soils with large pores, leverage for movement may be a problem.
- c) When water filled, large spaces may inhibit nematode movement (Wallace, 1958).

Mineral soils in all three of the habitats in this study are relatively coarse and overabundance of small pores is thus unlikely to be a problem. Furthermore, none of the samples examined were waterlogged (saturated with water); thus the contribution of increased particle size to the decrease in nematode populations likely reflects decreased availability of suitable water films for movement (perhaps due to the fact that coarse soils may lose water films more rapidly than finer soils).

In a review of various ecological studies, Sohlenius (1980) concluded that habitats may be ranked in order of increasing nematode abundance as follows: heathlands < coniferous forests < deciduous forests. The habitat rankings in terms of total nematode abundance obtained in this study (dry Kalmia heath-barren < black spruce-moss forest < Dryopteris-white birch forest) are consistent

with these conclusions. This may reflect the qualitative and quantitative differences among habitats in the composition of their soil microflora and microfauna, as affected by soil productivity (indicated by PC 1).

The Dryopteris-white birch stand has a luxurious vegetation cover (Appendix A) which provides an abundance of root systems for certain plant feeding nematodes. The high organic content in the decomposing humus layer and in the additional litter layer provides a diverse food source for microbial feeding, omnivorous, and in turn predatory nematodes. The black spruce-moss forest has a more reduced understory than the former habitat, while in the Kalmia heath-barren vegetation is sparse and soil organic content is very low. Thus, in both these habitats the food base available to nematodes is reduced.

The preponderance of microbial feeding taxa, followed by plant feeding, omnivorous, and predatory taxa, in the two forest sites studied is in keeping with general patterns reported for forest habitats (Twinn, 1962; Yuen, 1966; Egunjobi, 1971). There are no other nematological studies from heathlands similar to the one sampled in this study so it is difficult to evaluate the generality of the observed dominance of microbial feeders at this site. A similar pattern was observed in Dryas-dominated habitats (Kuzmin, 1976), but in Calluna-dominated sites in Britain, Banage (1966) found that plant feeding nematodes were dominant.

Total nematode populations and populations within all feeding groups decrease with soil depth. This concurs with all other ecological studies on

nematodes (Banage, 1966; Yuen, 1966; Egunjobi, 1971; Yeates, 1973, 1982; Wasilewska, 1974). This is probably due primarily to decreased soil productivity in the lower soil layers, but changes in soil particle size and temperature associated with increasing depth are also likely contributing factors. Others have shown that moisture, aeration, and temperature, (Bunt, 1954; Banage, 1966; Yuen, 1966; Egunjobi, 1968; Yeates, 1973; Brodie, 1976) and soil texture (Brodie, 1976; Boag, 1981) all vary with depth. It is not clear from these studies whether the effect of the above variables on nematode distribution can be separated from those associated with varying levels of soil organic content.

Microbial feeding nematodes are, as a group, most abundant, and the most important feeding group in the upper (FH and L) soil horizons. In addition, the vast majority of individual microbial feeding taxa are most abundant in the FH (and in some cases the L) soil horizons. This has also been observed in most other studies of nematode ecology (Yeates, 1967; Egunjobi, 1968; Wasilewska, 1974 and Ingham et al., 1985). Since microbial feeders feed predominantly on bacteria (Spaull, 1973d), their abundance in the FH and L horizons is understandable.

As a group, omnivorous nematodes are, like the microbial feeding taxa , most abundant and comprise a larger fraction of the total nematode fauna in the FH and L horizons. However, careful examination shows that this pattern is not consistent among taxa. Yeates (1967) and Wasilewska (1974) also note that there is no common pattern of vertical distribution among individual taxa in this feeding group. This may reflect the heterogeneous diet of these nematodes which may include bacteria, fungi, algae, higher plants, Protozoa, rotifers and possibly detritus (Spaull, 1973d).

The plant feeding group, although abundant in higher soil layers, constitutes a larger percentage of the nematode fauna in the lower (Ae and B) horizons. The increased frequency of plant parasitic nematodes in the lower soil depths has been noted by several other workers (Banage, 1966; Yeates, 1967; and Wasilewska, 1974). Some individual taxa in this group show very restricted habitat and vertical distributions. However, plant feeding taxa with more widespread distributions among habitats show no consistent among-species patterns of vertical distribution. Some species occur more abundantly in the higher soil layers, while others occur more abundantly in deeper ones. It has been suggested (Egunjobi, 1968; Baines et al., 1959) that distributions of plant feeding nematodes are largely determined by variation in root concentrations at different depths. It is likely that many of these species are specific to one or a few plant species, and this would account for some of the observed among-species differences in vertical and habitat distributions.

Predatory nematodes are usually few in number, and information on their distributions is scanty. In the habitats examined in this study, predatory nematodes are more abundant in the FH and L soil horizons. This is scarcely surprising since they are thought to feed predominantly on other members of the soil fauna (nematodes, enchytraeids, rotifers, tardigrades, and Protozoa), all of which are most numerous in the upper soil horizons.

Information on seasonal variation in nematode populations is often confusing and difficult to evaluate. Although sampling was carried out only from May through November (the ground was snow covered from mid-November until early

May in both 1986 and 1987), peaks in overall nematode populations occurred in mid-June and mid-September. Similar late spring/early summer and autumn peaks in populations were noted in mixed and spruce/fir forests of the Western Carpathians (Popovici, 1980), in English grasslands (Banage, 1966), and in Danish beech forests (Yeates, 1972). These peaks are most likely due to more pronounced physical and chemical changes in the soil at those times. Late spring/early summer peaks are probably due, at least in part, to increased egg hatching due to the onset of favourable environmental conditions, and temperature is likely to be particularily critical in this respect. Dramatic increases in food resources for most nematode groups (eg: new root growth, bacterial and fungal "blooms") also occur at this time, and are certainly a factor contributing to peaks in abundance. Fall peaks may be due to a build up of organic materials released from litter fall and from the senescence of annual plants.

Although individual nematode taxa show a wide variety of seasonal distributional patterns, many show one or other of these peaks, with some showing both. Different patterns are likely a result of differing life cycles and environmental tolerances which may in turn be partially cued to requirements for varying food sources.

It is clear from the Cluster and Discriminant Functions analyses that distinctive nematode assemblages occur in the habitats studied, and furthermore, that these assemblages have an ecological basis. However, a refined causal basis for the separation of these clusters is not available, since autecological knowledge of most of the nematode taxa encountered in this study is lacking.

The Cluster Analysis shows that the Kalmia heath-barren possesses a nematode assemblage that is clearly distinct from those found in the two forest habitats. Within the barrens site, however, soil layers appear to be relatively homogeneous with respect to the composition of their nematode fauna.

There is no clear separation of the two forest habitats on the basis of the nematode species present in each. Within these habitats, however, different soil layers appear to possess different nematode assemblages. The most distinctive of these is the litter layer of the Dryopteris-white birch forest, followed by the FH layers from both forest types. The two lower soil horizons from the forest stands appear relatively similar.

Two discriminant functions account for the ecological separation of the five major clusters that were revealed in the Cluster Analysis. The basis of separation on the first Discriminant Function is largely the separation of samples with higher pH and available P and relatively low levels of available K and N. The second Discriminant Function appears to reflect the ratio of soil water to organic content, as well as the amount of Mg relative to levels of Na and Ca.

The two assemblages that separate most strongly in discriminant space are clusters 4 and 5. The separation of Cluster 5 from the remaining groups is most apparent on Discriminant Function 2. The samples of this cluster are characterized by high organic content, relatively low moisture, and high Mg:Na and Mg:Ca ratios. This cluster includes all of the samples from the litter horizon of the Dryopteris-white birch stand. Given the high organic content of the samples it is not surprising that microbial taxa predominate in this assemblage.

Cluster 4 separates most strongly on Discriminant Function 1. This cluster is made up entirely of samples from the Kalmia heath-barren, and includes 14 of the 15 samples from this site. Soils in this habitat are characterized by low organic content, as well as generally low nutrient, and moisture levels. The low overall soil productivity implied by these characteristics is reflected in the low nematode diversity and abundance at this site.

Separation of clusters 1-3 in discriminant function space appear to reflect a gradient from upper soil to lower soil layers within the two forest habitats. Concomitant with increasing depth are trends towards less productive soils (i.e. with less organic material and generally lower nutrient levels). The changes in soil composition are reflected in changes in species composition. The upper (FH) horizon (Cluster 1), is characterized by an abundant and diverse fauna from all feeding groups. The lower soil layers (clusters 2 and 3), show reduced diversity of all feeding groups except plant feeding nematodes. These trends are easily understood in terms of food availability for species of the various feeding groups which characterize the assemblages.

The study of nematode ecology in natural ecosystems is still in need of much work. Sampling is difficult, and processing of samples is laborious. Thus, many studies are carried out on a small scale since large comparative studies are too time and resource intensive. In addition, the efficiency of extraction techniques varies, with no one technique equally suited for all nematode groups or for all soils.

Our knowledge of why nematodes occur in, or are more abundant in, some habitats than in others, is far from complete. The present work, for example, is the first study of nematode ecology (in natural ecosystems) in Newfoundland, and one of a few in Canada as a whole. The complexity of soil ecosystems makes a complete understanding of nematode-soil relationships difficult, and knowledge of chemical and physical soil factors only gives partial answers. Much more work on the autecology of individual nematode taxa is needed for a full understanding of interrelationships between nematodes and the environment in which they live. Filling these gaps in our knowledge will greatly increase our ability to predict nematode occurrence and abundance in natural ecosystems.

Chapter 5

LITERATURE CITED

Anonymous. 1986. SPSS-X Users Guide. McGraw-Hill, New York.

Baines, R.C., van Gundy, S.D. and S.A. Sher. 1959. Citrus and avocado nematodes. Calif. Agr. 13: 16-18.

Banage, W.B. 1963. The ecological importance of free-living soil nematodes with special reference to those of moorland soil. J. Anim. Ecol. 32: 133-140.

Banage, W.B. 1966. Nematode distribution in some British upland moor soils with a note on nematode parasitizing Fungi. J. Anim. Ecol. 35: 349-361.

Barker, K.R. 1985. Soil sampling methods and procedures for field diagnosis. In: Plant Nematology Laboratory Manual (Zuckerman, B.M.; Mai, W.F.; and M.B. Harrison Eds.). University of Massachusetts Agricultural Experimental Station, Amherst.

Bassus, W. 1962. Uber die Vertikalverteilung and den massenwechsel der nematoden in waldboden mitteldeutschlands. Nematologica 7:281-293.

Black, C.A. (Ed.). 1965. Methods of Soil Analysis. American Society of Agronamy, Madison, Wisconsin.

Boag, B. 1981. Observations on the population dynamics and vertical distribution of trichodorid nematodes in a Scottish forest nursery. Ann. Appl. Biol. 98: 463-469.

Brady, N.C. 1974. The Nature and Properties of Soils (8th edition). MacMillan, New York.

Braun-Blanquet, J. 1932. Plant Sociology: the Study of Plant Communities (Translated and edited by G.D. Fuller and H.C. Conard). McGraw-Hill, New York.

Brodie, B.B. 1976. Vertical distribution of three nematode species in relation to certain soil properties. J. Nematol. 8: 243-247.

Brzeski, M.W. and A. Dowe. 1969. Effect of pH on Tylenchorhynchus dubius (Nematoda: Tylenchidae). Nematologica 15: 403-407.

Bunt, J.S. 1954. The soil-inhabiting nematodes of Macquarie Island. Aust. J. Zool. 2:264-274.

Chitwood, B.G. and J. Feldmesser. 1948. Golden nematode population studies. Proc. Helminthol. Soc. Wash. 15: 43-55.

Coen, H. 1967. Notes on the host range, ecology and population dynamics of Pratylenchus brachyurus. Nematologica 13: 118-124.

Cohn, E. 1969. The occurrence and distribution of species of Xiphinema and Longidorus in Israel. Nematologica 15: 179-192.

Dropkin, V.H. 1980. Introduction to Plant Nematology. John Wiley and Sons, New York.

Dropkin, V.H., Martin, C.G. and R.W. Johnson. 1958. Effect of osmotic concentration on hatching of some plant parasitic nematodes. Nematologica 3: 115-126.

Egunjobi, O.A. 1968. An ecological study of some soil nematodes associated with apple trees in a New Zealand grassed orchard. N.Z. J. Agric. Res. 11: 386-406.

Egunjobi, O.A. 1971. Soil and litter nematodes of some New Zealand forests and pastures. N.Z. J. Sci. 14: 568-579.

Elliot, E.T., Anderson, R.V., Coleman, D.C. and C.V. Cole. 1980. Habitable pore space and microbial trophic interactions. Oikos 35: 327-335.

Elliot, J.M. and C.F. Marks. 1972. Control of nematodes in flue-cured tobacco in Ontario. Can. Dep. Agric. Publ. 1465.

Endo, B.Y. 1959. Responses of root lesion nematodes, Pratylenchus brachyurus and P. zeae, to various plants and soil types. Phytopathology 49: 417-421.

Ferris, H. and M.V. McKenry. 1976. A survey of nematode distribution in California vineyard soils. J. Amer. Soc. Hort. Sci. 101(3): 332-336.

Flegg, J.J.M. and D.J. Hooper. 1970. Extraction of free-living stages from soil. In:

Laboratory Methods for Work with Plant and Soil Nematodes Tech. Bull. No.2 (Southey, J.F., Ed.). Her Majesty's Stationery Office, London.

Freckman, D.W. and R. Mankau. 1977. Distribution and trophic structure of nematodes in desert soils. Ecol. Bull. (Stockholm) 25: 511-514.

Freckman, D.W., Duncan, D.A. and J.R. Larson. 1979. Nematode density and biomass in an annual grassland ecosystem. J. Range Manage. 32: 418-422.

Franz, H. 1942. Untersuchungen uber die Kleintierwelt ostalpiner Boden. I. Die Freilebenden Erdnematoden. Zool. Jahrb. Abt. Syst. 75: 365-546.

Godfrey, G.H. 1924. The depth distribution of the root-knot nematode Heterodera radicicola in Florida soils. J. Agric. Res. 29: 93-98.

Goodey, J.B. 1963. Laboratory Methods for Work with Plant and Soil Nematodes. Tech. Bull. Minist. Agri. Fish. Fd. No.2 (4th edition).

Goodey, T. (revised by Goodey, J.B.). 1963. Soil and Freshwater Nematodes. Methuen, London.

Green, R.H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. Ecology 52: 543-556.

Green R.H. and G.L. Vascotto. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12: 583-590.

Hooper, D.J. 1970. Handling, fixing, staining, and mounting nematodes. In: Laboratory Methods for Work with Plant and Soil Nematodes Tech. Bull. No.2 (Southey, J.F., Ed.). Her Majesty's Stationery Office, London.

Ingham, R.E., Anderson, R.V., Gould, W.D. and D.C. Coleman. 1985. Vertical distribution of nematodes in a short grass prairie. Pedobiologia 28: 155-160.

Johnson, P.W. and S.G. Fushtey. 1966. The biology of the Oat Cyst Nematode Heterodera avenae in Canada II. Nematode development and related anatomical changes in roots of oats and corn. Nematologica 12: 630-636.

Johnson, S.R., Ferris, J.M. and V.R. Ferris. 1972. Nematode community structure of forest woodlots. I. Relationships based on similarity coefficients of nematode species. J. Nematol. 4: 175-183.

Johnson, S.R., Ferris, J.M. and V.R. Ferris. 1973. Nematode community structure of forest woodlots. II. Ordination of nematode communities. J. Nematol. 5: 95-107.

Johnson, S.R., Ferris, J.M. and V.R. Ferris. 1974. Nematode community structure of forest woodlots. III. Ordinations of taxonomic groups and biomass. J. Nematol. 6: 118-126.

Jones, F.G.W. 1975. Accumulated temperature and rainfall as measures of nematode development and activity. Nematologica 21: 62-70.

Jones, F.G.W. and A.J. Thomasson. 1976. Bulk density as an indicator of pore space in soils usable by nematodes. Nematologica 22: 133-137.

Kable, P.R. and W.F. Mai. 1968. Influence of soil moisture on Pratylenchus penetrans. Nematologica 14: 101-122.

Kimpinski, J. and H.E. Welch. 1971. The ecology of nematodes in Manitoba soils. Nematologica 17: 308-318.

Kuzmin, L.L. 1976. Free-living nematodes in the tundra of western Taimyr. Oikos 27: 501-505.

Loof, P.A.A. 1971. Freeliving and plant parasitic nematodes from Spitzbergen, collected by Mr. H. van Rossen. Meded. LandbHoogesch. Wageningen 71: 1-86.

Mai, W.F. and M.B. Harrison. 1959. The Golden Nematode. Cornell Ext. Bull. 870.

McKeague, J.A. (Ed.) 1978. Manual on Soil Sampling and Methods of Analysis (2nd edition). Canadian Society of Soil Science.

Meagher, J.W. 1970. Seasonal fluctuations in numbers of larvae of the Cereal Cyst Nematode (Heterodera avenae) and of Pratylenchus minyus and Tylenchorhynchus brevidens in soil. Nematologica 16: 333-347.

Mountain, W.B. and H.R. Boyce. 1958. The peach replant problem in Ontario. VI. The relation of Pratylenchus penetrans to growth of young peach trees. Can. J. Bot. 36: 135-151.

Nielsen, C.O. 1949. Studies on the soil microfauna. II. The soil inhabiting nematodes. Nat. Jutlandica 2: 1-131.

Norton, D.C. 1963. Population fluctuations of Xiphinema americanum in Iowa. Phytopathology 53: 66-68.

Norton, D.C. 1979. Relationship of physical and chemical factors to populations of plant-parasitic nematodes. Ann. Rev. Phytopathol. 17: 279-299.

Norton, D.C., Frederick, L.R., Ponchillia, P.E. and J.W. Nyhan. 1971. Correlations of nematodes and soil properties in Soyabean fields. J. Nematol. 3: 154-163.

Ogiga, I.R. 1969. The distribution, seasonal population density and sex ratio of nematodes in an orchard (Unpub.). Macdonald College of McGill University, Montreal.

Ogiga, I.R. 1971. Environmental influences on nematode populations and studies on Tylenchorhynchus. M.Sc. Thesis McGill University, Montreal.

Ogiga, I.R. and R.H. Estey. 1973. Seasonal changes in population density, sex ratios and vertical distribution of nematodes in orchard soil. Phytoprotection 54: 57-68.

Olthof, Th.H.A., Marks, C.F. and J.M. Elliot. 1972. Relationship between population densities of Pratylenchus penetrans and crop losses in flue-cured tobacco in Ontario. J. Nematol. 5: 158-162.

Orr, C.C. and O.J. Dickerson. 1966. Nematodes in true prairie soils of Kansas. Trans. Kans. Acad. Sci. 69: 317-334.

Popovici, I. 1980. Distribution and dynamics of soil nematodes in mixed and spruce fir forest ecosystems. Rev. Roum. Biol. - Biol. Anim. 25: 171-179.

Roberts, B.A. 1977. The soils and vegetation of the Trailer Pond area (Avalon Peninsula), Newfoundland. In: The Physical Environment of the Trailer Pond Area (Avalon Peninsula) (Yollal, W.H., Ed.). Department of Geography, Memorial University of Newfoundland.

Roberts, B.A. 1983. Soils. In: Biogeography and Ecology of the Island of Newfoundland (South, G.R., Ed.). Junk, The Hague.

Rohlf, F.J. 1987. NTSYS-pc Version 1.3 Users Guide. Exeter, New York.

Salisbury, R.J. and J.E. Bosher. 1959. Nematode assays of some forest and nursery soils in British Columbia. Canada Forest Entomology and Pathology Branch Bi-monthly Progress Report 15: 4.

Schmitt, D.P. 1969. Population patterns of some stylet-bearing nematodes in a native Iowa prairie. J. Nematol. 1: 304.

Schmitt, D.P. and D.C. Norton. 1972. Relationships of plant parasitic nematodes to sites in native Iowa prairies. J. Nematol. 4: 200-206.

Seinhorst, J.W. 1956. Population studies on stem eelworms, (Ditylenchus dipsaci). Nematologica 1: 159-164.

Sheard, J.W. and D.W. Geale. 1983. Vegetation studies at Polar Bear Pass, Bathurst Island, N.W.T.. I. Classification of plant communities. Can. J. Bot. 61: 1618-1636.

Siddiqi, M.R. 1986. Tylenchida Parasites of Plants and Insects. Commonwealth Agricultural Bureaux, London.

Sohlenius, B. 1980. Abundance, biomass and contribution of energy flow by soil nematodes in terrestrial ecosystems. Oikos 4: 186-194.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. Freeman, New York.

Spaull, V.W. 1973a. Seasonal variation in the numbers of soil nematodes at Signy Island, South Orkney Islands. Br. Antarct. Surv. Bull. 33 & 34: 47-56.

Spaull, V.W. 1973b. Qualitative and quantitative distribution of soil nematodes of Signy Island, South Orkney Islands. Br. Antarct. Surv. Bull. 33 & 34: 177-184.

Spaull, V.W. 1973c. Distribution of soil nematodes in the maritime Antarctic. Br. Antarct. Surv. Bull. 37: 1-6.

Spaull, V.W. 1973d. Distribution of nematode feeding groups at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. Br. Antarct. Surv. Bull. 37: 21-32.

Sutherland, J.R. 1965. Nematodes associated with coniferous nursery seedlings in Quebec. Phytoprotection 46: 131-134.

Sutherland, J.R. 1967. Parasitism of Tylenchus emarginatus on conifer seedling roots and some observations on the biology of the nematode. Nematologica 13: 191-196.

Thorne, G. 1974. Nematodes of the Great Northern Plains. Part II Dorylaimoidea in part (Nemata: Adenophorea). S.D. Agric. Exp. Stn. Tech. Bull. No. 41.

Townshend, J.L. 1972. Influence of edaphic factors on penetration of corn roots by Pratylenchus penetrans and P. minyus in three Ontario soils. Nematologica 18: 201-212.

Twinn, D.C. 1962. The extraction of free-living nematodes from forest soil and litter. In: Progress of Soil Zoology (P.W. Murphy Ed.). Butterworths, London.

Wallace, H.R. 1958. Movement of eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm Heterodera schachtii Schmidt. Ann. Appl. Biol. 46: 74-85.

Wasilewska, L. 1971. Nematodes of the dunes in the Kampinos forest. II. Community structure based on numbers of individuals, state of biomass and respiratory metabolism. Ekol. Pol. 19: 651-688.

Wasilewska, L. 1974. Quantitative evaluation of the occurrence of nematodes in meadow soil from the surroundings of Sofia (Bulgaria). Zesz. Probl. Post. Nauk. Rdn. 154: 213-225.

Wells, R.E. and P.K. Heringa. 1972. Soil Survey of the Gander-Gambo Area, Newfoundland. Report No.1, Newfoundland Soil Survey. Agriculture Canada.

Willard, J.R. 1973. Soil invertebrates. V. Nematoda: Populations and biomass. Canadian Committee for the International Biological Programme, Matador Project, Saskatoon, Sask., Tech. Rep. 21.

Winslow, R.D. 1960. Some aspects of the ecology of free-living and plant-parasitic nematodes. pp 342-415 In: Nematology. Fundamentals and Recent Advances. (Sasser, J.N. and W.R. Jenkins Eds.) Univ. North Carolina Press, Chapel Hill.

Yeates, G.W. 1967. Studies on nematodes from dune sands 9. Quantitative comparison of the nematode faunas of six localities. N.Z. J. Sci. 10: 927-948.

Yeates, G.W. 1968. An analysis of annual variation of the nematode fauna in dune sand at Himatangi Beach, New Zealand. Pedobiologia 8: 173-207.

Yeates, G.W. 1972. Nematoda of a Danish beech forest 1. Methods and general analysis. Oikos 23: 178-189.

Yeates, G.W. 1973. Abundance and distribution of soil nematodes in samples from the New Hebrides. N.Z. J. Sci. 19:-727-736.

Yeates, G.W. 1974. Studies on a climosequence of soils in tussock grasslands 2. Nematodes. N.Z. J. Zool. 1: 171-177.

Yeates, G.W. 1979. Terrestrial nematodes from the Bunger Hills and Gaussberg, Antarctica. N.Z. J. Zool. 6: 641-643.

Yeates, G.W. 1982. Variation of pasture nematode populations over thirty-six months in a summer dry silt loam. Pedobiologia 24: 329-346.

Yuen, P.H. 1966. The nematode fauna of regenerated woodland and grassland of Broadbalk Wilderness. Nematologica 12: 195-214.

Appendix A

Site Description for Black Spruce-Moss Forest

Slope: 5-10%

Aspect: SE

Recent Disturbances: Windthrow

Origin: Fire

Successional Status: Disclimax, Climax

Homogeneity: Continuous

Microrelief: Hummocky

Microtopography: Middle Slope

Landforms: Glacial

Soil Type: Ortho Humo-Ferric Podzol (Roberts, 1983)

Soil Texture: Moderately Coarse, Medium

Soil Drainage: Well drained

Depth to bedrock: >1m

Exposure: Minimal

Depth to Watertable: >1m

Seepage: Slight

Appendix A continued

Vegetation List:	*Abundance Sociability
Abies balsamea (L.) Mill.	2.1
Bazzania trilobata (L.) S.F.Gray	2.2
Betula papyrifera Marsh.	1.1
Cornus canadenis L.	2.1
Dicranum majus Smith	2.2
Gaultheria hispidula (L.) Bigel.	2.2
Hylocomium splendens (Hedw.) B.S.G.	2.2
Monotropa uniflora L.	1.2
Nemopanthus mucronata (L.) Trel.	1.1
Picea mariana (Mill.) B.S.P.	4.1
Pleurozium schreberi (Brid.) Mitt.	3.3
Ptilium crista-castrensis (Hedw.) DeNot.	2.2
Sorbus americana Marsh.	1.1
Sphagnum sp. L.	2.2
Trientalis borealis Raf.	1.1

*Scale used in describing abundance and sociability taken from Braun-Blanquet, 1932.

Abundance/Cover:
- r- single specimen
- x- sparse
- 1- plentiful but covering <5%
- 2- abundant 5 to 25%
- 3- abundant 25 to 50%
- 4- abundant 50 to 75%
- 5- abundant >75%

Sociability:
1- singly
2- small groups or tufts
3- large groups or patches
4- extensive patches covering >50% of sample area
5- carpet covering >75% of sample area

Appendix B

Site Description for Dryopteris-White Birch Forest

Slope: 20-25%

Aspect: E 80°

Recent Disturbances: Fire, Cutting

Origin: Fire, Logging

Successional Status: Subclimax

Homogeneity: Patchy

Microrelief: Hummocky

Microtopography: Middle Slope

Landforms: Glacial

Soil Type: Intergrade between Ortho Homo-Ferric Podzol and Degraded Dystric-Brunisol (Roberts, 1983)

Soil Texture: Moderately Coarse, Medium

Soil Drainage: Moderately Well Drained

Depth to bedrock >1m

Exposure: Minimal

Depth to Watertable >1m

Seepage: Present

Appendix B continued

Vegetation List:	*Abundance Sociability
Abies balsamea (Mill.) B.S.P.	1.1
Bazzania trilobata (L.) S.F.Gray	2.2
Betula papyrifera Marsh.	3.1 to 4.1
Clintonia borealis (Ait.) Raf.	2.1
Cornus canadensis L.	3.1
Dicranum undulatum Brid.	2.2
Dryopteris spinulosa (O.F.Muell.) Watt	3.2
Hylocomium splendens (Hedw.) B.S.G.	2.2
Linnaea borealis L.	2.2
Monotropa uniflora L.	X.2
Nemopanthus mucronata (L.) Trel.	1.1
Pleurozium schreberi (Brid.) Mitt.	3.3
Sorbus americana Marsh.	1.1
Trientalis borealis Raf.	2.1

*Scale used in describing abundance and sociability taken from Braun-Blanquet, 1932.

Appendix C

Site Description for Dry Kalmia Heath-Barren

Recent Disturbances: Fire

Origin: Fire

Successional Status: Climax

Homogeneity: Continuous, Discontinuous

Microrelief: Hummocky

Microtopography: Upper Slope, Flat

Landforms: Glacial

Soil Type: Ortho Humo-Ferric Podozol (Roberts, 1983)

Soil Texture: Medium, Moderately Fine

Soil Drainage: Well Drained, Moderately Well Drained

Depth to Bedrock >1m

Exposure: Moderate

Depth to Watertable >1m

Seepage: Present

Appendix C continued

Vegetation:	*Abundance Sociability
Amelanchier bartramiana (Tausch) Roemer	1.1
Cetraria islandica (L.) Ach.	2.2
Cladonia alpestris	3.3
C. mitis (Sandst.) Hale and W.Culb.	2.2
C. rangiferina (L.) Wigg.	2.2
Clintonia borealis (Ait.) Raf.	X.1
Empetrum nigrum L.	2.2
Juniperus communis L.	1.3
Kalmia angustifolia L.	3.3
Ledum groenlandicum Oeder	2.1
Lycopodium annotinum L.	1.1
L. clavatum L.	1.2
L. obscurum L.	2.1 to 3.1
Maianthemum canadense Desfontaines	2.1
Nemopanthus mucronata (L.) Trel.	1.1
Orchis rotundifolia Pursh.	2.1
Polytrichum juniperinum Hedw.	1.2
Rhododendron canadense (L.) Torr.	3.2
Solidago sp. L.	X.1
Vaccinium angustifolium Ait.	2.2
V. vitis-idaea L.	2.1

*Scale used in describing abundance and sociability taken from Braun-Blanquet, 1932.

Appendix D

Seinhorst's Glycerol-Ethanol Method for Processing Nematodes (Goodey, 1963)

Transfer nematodes from fixative to a watch glass containing 0.5 ml of the following solution:

- 96% ethanol.....20 parts
- glycerol.....1 part
- distilled water.....79 parts

Place the watch glass in a closed glass vessel containing an excess of 96% ethanol and leave for at least 12 hours at 35-40°C. This will remove the water and leave the nematodes in a mixture of glycerol and ethanol.

Remove the watch glass from the vessel and fill it with a solution of 95 parts 96% ethanol and 5 parts glycerol. Leave in an open petri dish at 40°C until the ethanol has evaporated. Nematodes are then in pure glycerol and can be mounted.

Appendix E

Correlation Matrix of Mean Numbers of Nematodes and all Measured Environmental Variables

In the following table the abbreviations used are:

Nematodes-mean numbers of nematodes
Temp-temperature in °C
Org-soil organic content
N-available nitrogen
P-available phosphorus
K-available potassium
Na-available sodium
Ca-available calcium
Mg-available magnesium
Mo- soil moisture content
Size-soil particle size >2mm

All correlation values are significant at $p \leq 0.05$ with the exception of those marked with *.

	Nematode	Temp	pH	Org	N	P	K	Na	Ca	Mg	Mo	Size
Nematode	--											
Temp	.17*	--										
pH	-.75	-.03*	--									
Org	.79	.04*	-.63	--								
N	.76	.03*	-.52	.88	--							
P	.78	-.04*	-.71	.94	.80	--						
K	.86	.04*	-.71	.97	.88	.93	--					
Na	.79	.08*	-.73	.93	.81	.85	.94	--				
Ca	.79	.10*	-.82	.86	.72	.93	.87	.84	--			
Mg	.81	.05*	-.79	.95	.81	.94	.95	.95	.94	--		
Mo	.74	.01*	-.61	.90	.75	.80	.89	.91	.75	.87	--	
Size	-.48	-.40	.35	-.49	-.49	-.48	-.50	-.44	-.51	-.48	-.44	--

Appendix F

Nematode Taxa Recovered from Three Habitats in Butterpot Provincial Park

The following is a complete list of authorities for the taxa recovered from the three study sites.

TYLENCHIDA Thorne, 1949

Tylenchoidea (Oerley, 1880) Chitwood & Chitwood, 1937

Tylenchidae Oerley, 1880

Tylenchus sp.
Coslenchus costatus (de Man, 1921) Siddiqi, 1978
Malenchus exiguus (Massey, 1969) Andrassy, 1980
Ditylenchus sp.

Ecphyadophoridae Skarbilovich, 1959

Hoplolaimoidea (Filipjev, 1934) Paramonov, 1967

Pratylenchidae (Thorne, 1949) Siddiqi, 1963

Pratylenchus penetrans (Cobb, 1917) Filipjev & Schuurmans Stekhoven, 1941
Hirschmanniella sp.

Criconematoidea (Taylor, 1936) Goffart, 1966

Criconematidae (Taylor, 1936) Thorne, 1949

Neocrossonema menzeli (Stefanski, 1924) Ebsary, 1981
Nothocriconemella sphagni (Micoletzky, 1925) Ebsary, 1981

Ogma sp.
Seriespinula seymouri (Wu, 1965) Khan et al., 1976

Hemicycliophoroidea (Skarbilovich, 1959) Siddiqi, 1980

Hemicycliophoridae (Skarbilovich, 1959) Geraert, 1966

Hemicycliophora tenuis Thorne, 1955

Neotylenchoidea (Thorne, 1941) Jairajpuri & Siddiqi, 1969

Neotylenchidae Thorne, 1941

Deladenus sp.

Aphelenchoidea Fuchs, 1937 Thorne, 1949

Aphelenchoididae (Skarbilovich, 1947) Paramonov, 1953

Aphelenchoides sp.

RHABDITIDA (Oerley, 1880) Chitwood, 1933

Rhabditoidea (Oerley, 1880) Travassos, 1920

Rhabditidae Oerley, 1880

Bunonematidae (Micoletzky, 1922; Chitwood, 1935)
Paramonov, 1956

Bunonema richtersi Jagerskiold, 1905

Cephalobidae (Filipjev, 1934) Chitwood & Chitwood, 1934

Acrobeloides nanus (de Man, 1880) Anderson, 1968
Cephalobus sp.
Eucephalobus sp.

Diplogasteroidea (Micoletzky, 1922) Goodey, 1963

Diplogasteridae (Micoletzky, 1922) Steiner, 1929

Micoletzky sp.

TERATOCEPHALIDA (Andrassy, 1958) Goodey, 1963

Teratocephalidae Andrassy, 1958

Euteratocephalus sp.
Teratocephalus sp.1
Teratocephalus sp.2

ARAEOLAIMIDA Schuurmanns Stekhoven & de Coninck, 1933

Plectoidea (Oerley, 1880) Chitwood, 1937

Plectidae Oerley, 1880

Plectus acuminatus Bastian, 1865
Plectus sp.
Wilsonema sp

MONHYSTERIDA (Oerley, 1880)

Monhysteridae (Oerley, 1880) Shuurmans Stekhoven & de Coninck, 1933

Eumonhystera sp.
Prismatolaimus dolichurus de Man, 1880

CHROMADORIDA (Filipjev, 1917) Chitwood, 1933

Cyatholaimidae (Micoletzky, 1922) Schuurmans Stekhoven & de Coninck, 1933

Achromadora ruricola (de Man, 1880) Micoletzky, 1925

DORYLAIMIDA (de Man, 1876) Pearse, 1942

Dorylaimoidea (de Man, 1876) Thorne, 1934

Dorylaimidae de Man, 1876

Eudorylaimus carteri (Bastian, 1865) Andrassy, 1959

Eudorylaimus sp.
Mesodorylaimus sp.
Prodorylaimus sp.

Aporcelaimidae Heyns, 1965

Aporcelaimellus capitatus (Thorne & Swanger, 1936) Heyns, 1965
Thonus elegans Thorne, 1974

Tylencholaimidae (Filipjev, 1934) Siddiqi, 1969

Tylencholaimus nanus Thorne, 1939
Tylencholaimus sp.

Nygolaimidae (Thorne, 1935) Meyl, 1961

Paravulvulus planposae (Altherr, 1952) Thorne, 1974

Mononchoidea (Chitwood, 1937) Clark, 1961

Mononchidae Chitwood, 1937

Mononchus sp.
Mylonchulus brevicaudatus (Cobb, 1917) Altherr, 1954
Prionchulus punctatus (Cobb, 1917) Clark, 1960

Alaimoidea (Micoletzky, 1922) Goodey, 1963

Alaimus primitivus de Man, 1880 (Microbial)

Diptherophoroidea (Thorne, 1935) Clark, 1961

Diptherophoridae Thorne, 1935

Diptherophora sp.

*Unidentified A
*Unidentified B

* As only juveniles were present identification was not possible.

Appendix G

Seasonal and Vertical Distribution of Infrequent or Highly Restricted Taxa

The following tables give the seasonal and vertical distribution of abundance for all nematode taxa that were not discussed in detail in the main body of the thesis. Values given for each layer and time are nematodes/500 mls of soil. Sites are as follows: 1- black spruce-moss forest; 2- Dryopteris-white birch forest; 3- Kalmia heath-barren.

Table G-1: Vertical and seasonal distribution of Hirschmanniella sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	37	37
2	FH	-	-	-	-	-	--
	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	37	37
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-2: Vertical and seasonal distribution of Deladenus sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	34	-	23	44	60	161
1	Ae	9	-	-	-	2	11
	B	12	-	-	2	22	36
Total		55	-	23	46	84	208
	L	-	-	-	40	-	40
2	FH	17	-	-	-	-	17
	Ae	-	33	-	-	-	33
	B	-	-	-	-	-	--
Total		17	33	-	40	-	90
	FH	6	-	-	-	-	6
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		6	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-3: Vertical and seasonal distribution of Neocrossonema menzeli at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	54	68	11	29	-	162
1	Ae	9	11	7	2	4	33
	B	12	-	-	-	-	12
Total		75	79	18	31	4	207
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	FH	-	-	-	-	3	3
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	3	--

Dashes indicate the taxon was absent.

Table G-4: Vertical and seasonal distribution of Pratylenchus penetrans at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	8	-	-	-	-	8
1	Ae	25	3	7	2	13	50
	B	107	54	7	58	5	231
Total		140	57	14	60	18	289
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	7	-	-	4	-	11
	B	8	-	6	-	-	14
Total		15	-	6	4	-	25
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-5: Vertical and seasonal distribution of Ecphyadophoridae at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	80	44	10	24	8	162
	B	39	-	9	-	43	91
Total		119	44	19	24	51	253
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	3	-	-	-	-	3
Total		3	-	-	-	-	3

Dashes indicate the taxon was absent.

Table G-6: Vertical and seasonal distribution of Ogma sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	-	--
2	FH	11	-	-	20	-	31
	Ae	7	14	8	4	7	40
	B	-	-	3	-	-	3
Total		18	14	11	24	7	74
	FH	-	-	5	-	-	5
3	Ae	-	-	-	-	-	--
	B	-	-	-	2	2	4
Total		-	-	5	2	2	9

Dashes indicate the taxon was absent.

Table G-7: Vertical and seasonal distribution of Nothocriconemella sphagni at the three study sites (1987).

		Sampling Time					
		May	Jun	Aug	Sept	Nov	Total
		13	21	2	13	1	
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	-	--
2	FH	11	93	-	-	13	117
	Ae	84	122	28	37	28	299
	B	16	25	29	-	-	70
Total		111	240	57	37	41	486
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	7	-	-	-	-	7
Total		7	-	-	-	-	7

Dashes indicate the taxon was absent.

Table G-8: Vertical and seasonal distribution of Ditylenchus sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	2	2
	B	-	-	-	-	-	--
Total		-	-	-	-	2	2
	L	32	103	499	358	591	1583
2	FH	-	16	-	39	-	55
	Ae	-	-	-	4	2	6
	B	-	5	-	-	12	17
Total		32	124	499	401	605	1661
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	1	-	-	1
Total		-	-	1	-	-	1

Dashes indicate the taxon was absent.

Table G-9: Vertical and seasonal distribution of Seriespinula seymouri at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	10	-	-	-	10
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	10	-	-	-	10
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	FH	30	34	26	37	3	130
3	Ae	-	-	4	2	2	7
	B	3	5	13	4	9	34
Total		33	39	43	43	14	171

Dashes indicate the taxon was absent.

Table G-10: Vertical and seasonal distribution of Tylencholaimus nanus at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	4	-	4	-	8
Total		-	4	-	4	-	8
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	-	-	-	-	-	--
	B	8	30	15	47	4	104
Total		8	30	15	47	4	104
	FH	24	6	-	-	-	30
3	Ae	-	-	-	-	-	--
	B	-	-	-	4	-	4
Total		24	6	-	4	-	34

Dashes indicate the taxon was absent.

Table G-11: Vertical and seasonal distribution of Thonus elegans at the three study sites (1987).

		Sampling Time					
		May	Jun	Aug	Sept	Nov	Total
		13	21	2	13	1	
Site	Layer						
	FH	17	-	23	-	-	40
1	Ae	9	-	-	-	-	9
	B	12	-	-	-	-	12
Total		38	-	23	-	-	61
	L	6	-	-	-	-	6
2	FH	11	108	25	78	19	241
	Ae	-	4	3	4	25	36
	B	-	-	-	3	-	3
Total		17	112	28	85	44	286
	FH	18	20	26	16	18	98
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	2	2
Total		18	20	26	16	20	100

Dashes indicate the taxon was absent.

Table G-12: Vertical and seasonal distribution of Prodorylaimus sp. at the three study sites (1987).

		Sampling Time					
		May	Jun	Aug	Sept	Nov	Total
		13	21	2	13	1	
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	2	2
	B	6	4	2	6	2	20
Total		6	4	2	6	4	22
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	4	-	-	4	2	10
	B	31	5	6	3	12	57
Total		35	5	6	7	14	67
	FH	24	-	-	-	-	24
3	Ae	2	-	-	-	-	2
	B	3	-	-	-	-	3
Total		29	-	-	-	-	29

Dashes indicate the taxon was absent.

Table G-13: Vertical and seasonal distribution of Aporcelaimellus capitatus at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	3	-	-	2	5
	B	-	4	-	-	-	4
Total		-	7	-	-	2	9
	L	-	-	-	-	-	--
2	FH	-	16	-	-	-	16
	Ae	4	4	-	-	-	8
	B	8	5	3	7	12	35
Total		12	25	3	7	12	59
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-14: Vertical and seasonal distribution of Paravulvulus planposae at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	42	24	34	-	18	118
1	Ae	-	7	-	-	2	9
	B	6	4	-	-	-	10
Total		48	35	34	-	20	137
	L	12	-	8	-	-	20
2	FH	261	16	8	39	174	498
	Ae	18	-	5	13	8	44
	B	-	-	-	-	-	--
Total		291	16	21	52	182	562
	FH	105	375	197	203	♀	889
3	Ae	-	4	1	2	-	7
	B	-	3	-	2	-	5
Total		105	382	198	207	9	901

Dashes indicate the taxon was absent.

Table G-15: Vertical and seasonal distribution of Eucephalobus sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	11	-	-	11
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	11	-	-	11
	L	-	-	-	-	-	--
2	FH	-	-	-	-	-	--
	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-16: Vertical and seasonal distribution of Micoletzky sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	5	5
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	5
	L	-	-	-	-	-	--
2	FH	11	-	-	-	-	11
	Ae	-	-	-	-	-	--
	B	-	-	-	-	3	3
Total		11	-	-	-	3	14
	FH	-	6	-	-	-	6
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	6	-	-	-	6

Dashes indicate the taxon was absent.

Table G-17: Vertical and seasonal distribution of Achromadora ruricola at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	5	5
1	Ae	-	5	3	-	-	8
	B	-	13	15	6	-	34
Total		-	18	18	6	5	47
	L	-	-	-	-	-	--
2	FH	11	-	-	-	13	24
	Ae	-	4	-	-	-	4
	B	-	-	-	-	21	21
Total		11	4	-	-	34	49
	FH	-	6	-	46	12	64
3	Ae	-	-	1	7	-	8
	B	-	-	-	10	-	10
Total		-	6	1	63	12	82

Dashes indicate the taxon was absent.

Table G-18: Vertical and seasonal distribution of Bunonema richtersi at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	5	5
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	25	27	-	52
2	FH	11	-	25	39	13	88
	Ae	-	-	3	-	8	11
	B	-	-	-	-	-	--
Total		11	-	53	66	21	151
	FH	24	-	5	-	-	29
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		24	-	5	-	-	29

Dashes indicate the taxon was absent.

Table G-19: Vertical and seasonal distribution of Rhabditidae at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	8	-	-	-	71	79
1	Ae	-	-	3	-	-	3
	B	6	-	-	-	-	6
Total		14	-	3	-	71	88
	L	164	11	-	-	-	175
2	FH	272	16	-	392	206	886
	Ae	84	22	5	-	8	119
	B	-	35	3	10	26	74
Total		520	84	8	402	240	1254
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-20: Vertical and seasonal distribution of Teratocephalus sp.1 at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	8	10	80	20	5	123
1	Ae	-	-	-	-	4	4
	B	6	4	-	2	-	12
Total		14	14	80	22	9	139
	L	18	113	-	66	24	221
2	FH	-	46	34	-	-	80
	Ae	4	11	-	-	-	15
	B	-	-	-	-	-	--
Total		22	170	34	66	24	316
	FH	30	6	10	22	-	68
3	Ae	-	3	-	-	-	3
	B	-	-	1	-	-	1
Total		30	9	11	22	-	72

Dashes indicate the taxon was absent.

Table G-21: Vertical and seasonal distribution of Wilsonema sp. at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	25	10	-	-	-	35
1	Ae	-	-	-	-	-	--
	B	-	4	-	-	-	4
Total		25	14	-	-	-	39
	L	115	11	25	279	5	435
2	FH	11	140	51	20	45	267
	Ae	-	4	-	4	-	8
	B	-	5	-	-	4	9
Total		126	160	76	303	49	719
	FH	36	14	10	-	-	60
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-22: Vertical and seasonal distribution of Unknown sp.1 at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	-	-
2	FH	-	-	-	-	-	--
	Ae	-	11	-	-	2	13
	B	-	195	15	99	47	356
Total		-	206	15	99	49	369
	FH	-	-	-	-	-	--
3	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--

Dashes indicate the taxon was absent.

Table G-23: Vertical and seasonal distribution of Unknown sp. 2 at the three study sites (1987).

		Sampling Time					
		May 13	Jun 21	Aug 2	Sept 13	Nov 1	Total
Site	Layer						
	FH	-	-	-	-	-	--
1	Ae	-	-	-	-	-	--
	B	-	-	-	-	-	--
Total		-	-	-	-	-	--
	L	-	-	-	-	-	--
2	FH	11	-	-	-	-	11
	Ae	18	14	3	26	17	78
	B	8	5	9	3	4	29
Total		37	19	12	29	21	118
	FH	71	6	5	6	18	106
3	Ae	5	3	-	5	6	19
	B	10	-	-	18	23	51
Total		86	9	5	29	47	176

Dashes indicate the taxon was absent.